U.S. Department
of Commerce

Volume 100
Number 1
January 2002

Fishery Bulletin

U.S. Department of Commerce

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The *Fishery Bulletin* (ISSN 0090-0656) is published quarterly by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, BIN C15700, Seattle, WA 98115-0070. Periodicals postage is paid at Seattle, WA, and at additional mailing offices. POSTMASTER: Send address changes for subscriptions to Fishery Bulletin, Superintendent of Documents, Attn.: Chief, Mail List Branch, Mail Stop SSOM, Washington, DC 20402-9373.

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The Secretary of Commerce has determined that the publication of this periodical is necessary according to law for the transaction of public business of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget.

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. Subscription price per year: $45.00 domestic and $56.25 foreign. Cost per single issue: $28.00 domestic and $35.00 foreign. **See back for order form.**

Fishery Bulletin

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101 Pivers Island Road
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Scientific Publications Office
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U.S. Department
of Commerce
Seattle, Washington

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Abstract–Otolith thermal marking is an efficient method for mass marking hatchery-reared salmon and can be used to estimate the proportion of hatchery fish captured in a mixed-stock fishery. Accuracy of the thermal pattern classification depends on the prominence of the pattern, the methods used to prepare and view the patterns, and the training and experience of the personnel who determine the presence or absence of a particular pattern. Estimating accuracy rates is problematic when no secondary marking is available and no error-free standards exist. Agreement measures, such as *kappa* (κ), provide a relative measure of the reliability of the determinations when independent readings by two readers are available, but the magnitude of κ can be influenced by the proportion of marked fish. If a third reader is used or if two or more groups of paired readings are examined, latent class models can provide estimates of the error rates of each reader. Applications of κ and latent class models are illustrated by a program providing contribution estimates of hatchery-reared chum and sockeye salmon in Southeast Alaska.

Manuscript accepted 16 April 2001.
Fish. Bull. 100:1–10 (2002).

The use of agreement measures and latent class models to assess the reliability of classifying thermally marked otoliths*

D. James Blick
Peter T. Hagen

Alaska Department of Fish and Game
Division of Commercial Fisheries
10107 Bentwood Place
Juneau, Alaska 99802-5526

E-mail address (for P. T. Hagen, contact author): peter_hagen@fishgame.state.ak.us

The ability to induce patterns in salmon otoliths by manipulating water temperatures has proved to be an efficient means for marking large numbers of salmon (Volk et al., 1990). When salmon embryos or alevins are exposed to a rapid drop in temperature, otolith growth is temporarily disrupted, and this results in a discontinuity in the otolith's microstructure. When viewed under transmitted light microscopy, this discontinuity appears as a dark ring. By controlling the number of temperature drops and the timing between drops, a coded pattern of dark rings can be recorded on the otolith and this pattern can be recovered from otoliths of older fish by removing the overlaying material and exposing the otolith core. For hatcheries that release a large number of fish, this type of marking method has shown to be particularly cost effective for marking 100% of the releases (Munk et al., 1993).

Several fisheries management programs in Alaska use thermal marking to estimate hatchery contributions to commercial fisheries (Hagen et al., 1995). Typically, several hundred salmon otoliths are systematically collected during each two- or three-day commercial opening during the fishing season. The otoliths and sampling data are shipped to a processing laboratory where a subsample of otoliths (generally 50 to 100) are processed immediately to meet in-season management needs; a portion of the remaining otoliths are processed later to provide an overall estimate of hatchery contribution to the fisheries.

The process by which a reader determines the presence or absence of a thermal mark in an otolith can be characterized as one of pattern recognition and image matching. Prior to examining otoliths of unknown origin, the readers gain familiarity with the patterns likely to be encountered by carefully examining fry otoliths that were obtained after thermal marking but prior to their release into the wild. Because there can be wide variation in the appearance of the thermal marks within a mark group (due in part to differences in developmental stages at marking), a single mark group may be represented by a variety of patterns. As a result, secondary characteristics and measurements of the patterns are sometimes necessary to identify an otolith to a mark group. The examination is also used to confirm that all the hatchery fish have been successfully marked.

The process of making a determination on otoliths from returning adult salmon can become problematic because wild salmon may also contain otolith patterns that can mimic the features imposed through thermal marking. Referred to as "noisy patterns," their presence can increase the rate of false positives. Conversely, if the hatchery employs poor temperature control or unintended disruptions occur around the period of marking, it may be difficult to identify the otolith as that of a

* Contribution PP-184 of the Alaska Department of Fish and Game, Commercial Fisheries Division, Juneau, Alaska 99802-5526.

hatchery fish, and this would increase the rate of false negatives. Differences between readers in skill and training level, and how they process otoliths, can add to the uncertainty in estimating the accuracy of the readings and the rates of false positives and negatives.

Otolith marking generally takes place without any secondary marking, such as fin-clipping or coded-wire-tagging; therefore the accuracy of a reading cannot directly be determined through conventional methods that make use of a "gold standard" (known origin sample) or other error-free classification methods. To ensure that the information provided to the Alaskan fisheries managers is accurate, each otolith is independently examined by two readers, and a third reading is used to resolve differences between the first two readings. The resolved readings are used to estimate the contribution of hatchery fish, and the presumption of accuracy is based on the premise that, through multiple readings, all marked fish are either correctly identified or that errors, if present, are inconsequential. Developing the analytical tools to determine the veracity of that assumption is the objective of this investigation, and by establishing such tools, quality control standards for recovering thermal marks can be developed.

In developing the tools to measure the quality of otolith readings, three questions are addressed:

1 How to assess the reliability of otolith readings when no standards are available.
2 How to estimate the proportion of hatchery marks when there is disagreement between two or more readers.
3 How the precision of the estimate of the proportion is influenced by classification error.

We discuss two approaches: 1) indices of agreement typically used in reliability studies, and 2) latent class models where classification errors are estimated for each reader even though the true error rate is considered unknown. The data requirements and their attendant assumptions are presented for each approach. The methods are illustrated by examining among-reader comparisons of chum salmon (*Oncorhynchus keta*) and sockeye (*Oncorhynchus nerka*) salmon otoliths collected from programs that monitor inseason contributions of hatchery fish in several commercial fisheries in Southeast Alaska (Hagen et al., 1995). The results are used to provide recommendations for monitoring the quality of otolith readings for thermal marking programs.

Methods

Standard available

A sample of n otoliths, which are examined by two readers, can be cross-classified as hatchery (H) or wild stock (W) as in Table 1. Suppose we wish to estimate the accuracy rate (probability of making a correct classification) or conversely, the error rate (probability of making a wrong classification). If we know nothing about reader 1, but reader 2 is infallible (or is considered a "gold standard"), unbiased estimates of the accuracy and error rates of reader 1 and the proportion of hatchery stocks (p) are given by

$$\hat{\pi}^{(1)}_{H|H} = n_{HH}/n_{H}, \qquad \hat{\pi}^{(1)}_{W|H} = n_{WH}/n_{H} = 1-\hat{\pi}_{H|H}$$
$$\hat{\pi}^{(1)}_{W|W} = n_{WW}/n_{W}, \qquad \hat{\pi}^{(1)}_{H|W} = n_{HW}/n_{W} = 1-\hat{\pi}_{W|W}$$
$$\hat{p} = n_{H}/n,$$

(where, for example, $\pi^{(1)}_{W|H}$ refers to the probability that reader 1 classifies an otolith as W when its true state is H). These estimates reflect the fact that reader 2 is infallible; the accuracy rates ($\hat{\pi}_{H|H}$, $\hat{\pi}_{W|W}$) and the error rates ($\hat{\pi}_{W|H}$, $\hat{\pi}_{H|W}$) are conditional on the numbers of hatchery or wild stock otoliths as determined by reader 2.

Table 1

Notation used to show the cross-classification of a sample of n otoliths by two readers to either hatchery (H) or wild stock (W) assignment. Row and column sums are indicated by the subscript "·"

		Reader 2		
		H	W	
Reader 1	H	n_{HH}	n_{HH}	$n_{H\cdot}$
	W	n_{WH}	n_{WW}	$n_{W\cdot}$
		$n_{\cdot H}$	$n_{\cdot W}$	n

No standard available

If a standard is not available, an unbiased estimate of p can be obtained if the accuracy rates for reader 1 are known. The estimate is

$$\hat{p}^{*} = (n_{H}/n + \pi^{(1)}_{W|W} - 1)/(\pi^{(1)}_{H|H} + \pi^{(1)}_{W|W} - 1),$$

where n_H is the number of otoliths classified as hatchery otoliths. If the accuracy rates are estimated, then $\hat{p}^{*}$ will no longer be unbiased, but will be much less biased than the estimator n_H/n and will in general have a much smaller mean-squared error (Rogan and Gladen, 1978). For a Bayesian approach to this problem, see Viana et al. (1993) and Joseph et al. (1995).

Agreement measures When accuracy rates are unavailable, statistics that measure "agreement" between readers are often calculated (e.g. Fleiss, 1981). One such index is simply the proportion of observed agreement (P_o), defined as

$$P_{o} = (n_{HH} + n_{WW})/n.$$

Another index, called *kappa* (κ), corrects P_o for the degree of agreement that is expected by chance alone. It is defined as

$$\kappa = (P_o - P_e)/(1 - P_e),$$

where P_e = expected agreement = $(n_H n_{\cdot H} + n_W n_W)/n^2$. The divisor, $1 - P_e$, constrains κ to be less than or equal to one, and if all agreement is due to chance (P_o=P_e), then κ equals zero. Note that with κ, independence between readers is assumed in order to calculate expected agreement.

An example of how agreement indices can be used to monitor readings is shown in Figure 1, which displays κ and its standard error for 2874 chum otoliths readings divided into 27 groups based on different reader pairs and capture locations. Included are P_o's for four of the groups. The results indicate that κ levels were similar between the different groups, suggesting overall consistency in readings, although some of the groups had lower values, which in practice would invite further investigation.

The P_o's in Figure 1 have a different rank order than the κ values. This apparent discrepancy highlights a potential problem in interpretation when using agreement indices to draw conclusions. To help illustrate this point, consider the following examples (Table 2). Table 2A is generated as the expected counts, given $\pi_{H|H} = 0.9$ and $\pi_{W|W} = 1.0$ for both readers, and $p = 0.1$. In this case, $P_o = 0.98$ and $\kappa = 0.89$. On the other hand, Table 2B is generated under the same assumptions except that $\pi_{H|H} = 0.5$. In this case P_o drops only slightly to 0.95, whereas κ drops to 0.47. Because the hatchery stock is rare, the inability of the readers to detect the mark is not well reflected by P_o, whereas κ reflects it better by correcting for the high level of chance agreement.

Now let $\pi_{H|H} = 0.9$ and $\pi_{W|W} = 0.9$ for both readers, and P= 0.5 (Table 2C). In this case, $P_o = 0.82$ and $\kappa = 0.64$. On the other hand, Table 2D is generated under the same assumptions except that P= 0.05. In this case, P_o remains unchanged at 0.82, but κ drops to 0.25.

In none of the above examples is the index "wrong." Rather, as is the case with most indices, interpretation is affected by the values of the underlying parameters. In the latter example (Table 2, C–D), even though P_o is the same for C and D, the scale it is being compared with has changed, thus changing the value of κ. This increases the difficulty of comparing κ across populations with different underlying proportions. Note also that Table 2D could have been derived from $\pi_{H|H} = 0.5$ and $\pi_{W|W} = 0.944$ for both readers, and $p = 0.19$. Thus, without additional information, it is impossible to draw reliable conclusions about reader accuracies or the proportion of hatchery marks.

Although agreement measures can be ambiguously interpreted, in practice they can still serve a useful monitoring role during routine comparisons when the circumstances of the readings are fairly well characterized. The interpretive difficulties with indices such κ and P_o become apparent when trying to translate agreement measures into statements about the accuracy of different readers and about the influence of reading error on the contribution estimates.

Latent class models An alternative approach is to try to estimate $\pi_{H|H}$ and $\pi_{W|W}$ for each reader, along with p. Although at first thought this may seem impossible, it can be shown that either by setting a few constraints or by collecting additional information, estimation is indeed possible. This problem falls into the category of latent class modeling (e.g. Everitt, 1984; Bartholomew, 1987; McCutcheon, 1987; Clogg, 1995). Latent class models (LCMs) belong to a family of latent variable models that hypothesize the existence of unobservable "latent" variables, about which information can be obtained only though measurements on observable "manifest" variables. LCMs specifically restrict the latent and manifest variables to be categorical. In the present situation, the latent variable is the true class (H or W) to which the otolith belongs, whereas the manifest variables are the readers' classifications. Such models have been used for assessing reliability of diagnostic tests in the medical field over the last 20 years (see Walter and Irwig, 1988; Formann, 1996, for reviews).

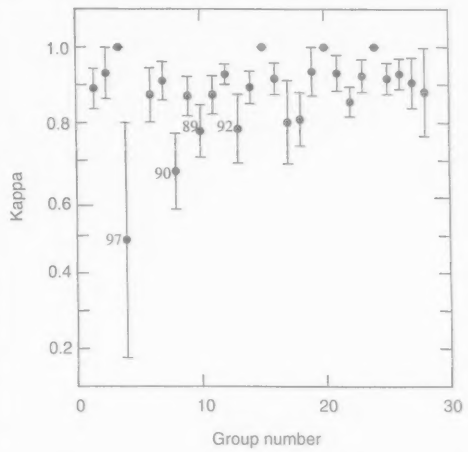

Figure 1

The values of κ (±1 SE) from 27 groups of paired readings of chum salmon otoliths (total=2874). The groups are based on pairs of different readers examining otoliths collected at different times and locations. The proportion of agreement (P_o) is shown next to group 4, 7, 9, and 12 for comparison with the value of κ.

Returning to the problem with two readers, neither of which is a standard, there are five essential parameters to estimate: $\pi^{(1)}_{H|H}, \pi^{(2)}_{H|H}, \pi^{(1)}_{W|W}, \pi^{(2)}_{W|W}$, and p, with only 3 df (four pieces of data, n_{HH}, n_{HW}, n_{WH}, n_{WW}, minus one because the sample size, n, is fixed). Thus, the model is overparameterized, and either constraints on the parameters or more data are needed. Possible constraints include 1) considering that two of the parameters are known (e.g. $\pi^{(1)}_{W|W} = \pi^{(2)}_{W|W} = 1$; i.e. both readers always call a wild stock correctly, there are no "false positives"), or 2) considering that two sets of parameters are equal (e.g. $\pi^{(1)}_{H|H}, \pi^{(2)}_{H|H}, \pi^{(1)}_{W|W} = \pi^{(2)}_{W|W}$; i.e. the accuracy rates are the same for both readers).

Although there may be times when such constraints are realistic, in general they will not be; therefore more infor-

mation will be necessary. One way to generate more information is to have a third independent reader (Walter, 1984). With three readers, there are seven essential parameters: $\pi_{H|H}^{(1),(2),(3)}$, $\pi_{W|W}^{(1),(2),(3)}$ and p. There is also $2^3 - 1 = 7$ df, so that all the parameters are estimable. Estimation is most commonly done by the method of maximum likelihood.

If readings are assumed to be independent among readers and among otoliths, the likelihood function is

$$\prod_{i=H,W}\prod_{j=H,W}\prod_{k=H,W}\left\{p\pi_{i|H}^{(1)}\pi_{j|H}^{(2)}\pi_{k|H}^{(3)}+(1-p)\pi_{i|W}^{(1)}\pi_{j|W}^{(2)}\pi_{k|W}^{(3)}\right\}^{n_{ijk}}.$$

This likelihood function must be maximized numerically and methods for this computation will be discussed later.

If more than three readers are used, there are extra degrees of freedom that can be used to assess goodness-of-fit. For example, with four readers there will be nine parameters with 15 df, leaving 6 df for goodness-of-fit. Pearson chi-square or likelihood ratio G^2 tests would both be applicable.

Another way to generate additional information was proposed by Hui and Walter (1980). Suppose there are two or more strata with different hatchery proportions in each strata. For example, catch could be stratified temporally or spatially. If it is assumed that $\pi_{H|H}^{(k)}$ and $\pi_{W|W}^{(k)}$ remain constant over strata, then a solution for just two readers may be obtained. For example, if there are two readers and two strata, then there are six parameters: $\pi_{H|H}^{(1),(2)}$, $\pi_{W|W}^{(1),(2)}$, p_1, and p_2, with $2(2^2 - 1) = 6$ df. Increasing the number of strata increases the degrees of freedom; e.g. three strata for two readers gives $3(2^2 - 1) = 9$ df for 7 parameters. The likelihood function for two readers and S strata is

$$\prod_{g=1}^{S}\prod_{i=H,W}\prod_{j=H,W}\left\{p_g\pi_{i|H}^{(1)}\pi_{j|H}^{(2)}+(1-p_g)\pi_{i|W}^{(1)}\pi_{j|W}^{(2)}\right\}^{n_{ijg}}.$$

A third way to supply additional information is to take a Bayesian approach (see "Discussion" section). By specifying prior distributions of the model parameters, unique estimates can be obtained (Joseph et al., 1995).

A critical assumption in the above models is that readings are independent. Specifically, the reading of each otolith by a given reader is independent of any other reading by the same reader, and each reading by various readers on a given otolith is independent given the true state of the otolith. In principle, the latter assumption may be difficult to meet especially if all readers examine the same otolith. The fact that the otolith is not prepared independently by each reader could induce a dependence among the readers. Also, variability in the readability of the mark due to the marking process can induce a dependence. Such dependence can bias the estimators of π and p (Vacek, 1985). Note that this latter assumption of independence is also required for κ.

One remedy for the problem of dependence due to preparation is to require independent preparations. This however, requires additional otoliths and with only two otoliths per fish, this would limit the number of readers to two. But in practice, this may not be a large concern. Typically, the second reader has the option to provide additional processing effort to the first otolith or, if needed, to process the second otolith. In almost all cases additional preparation is not done and readers feel they are able to extract sufficient information about the presence or absence of a mark from each other's preparations. In addition, reader accuracy rates obtained by LCM do not appear to vary systematically with the reading order, which also suggests that preparation-induced dependency is not a significant factor.

Dependency associated with variability in the appearance of the mark may be harder to address. A general solution is to model the dependence with additional parameters (e.g. Vacek, 1985; Qu et al., 1996; Yang and Becker, 1997; Qu and Hagdu; 1998; Albert et al., 2001). Modeling dependence requires either more readers or more strata. These modeling approaches are complicated and are currently evolving (see Albert et al., 2001). Alternatively, ad-

Table 2

Examples from cross-classification data generated as expected counts from a sample of 1000 otoliths based on different accuracy rates for identifying hatchery fish ($\pi_{H|H}$) and wild fish ($\pi_{W|W}$) under different mark proportions (p). The examples used illustrate differences between observed agreement (P_o) and chance-corrected agreement (κ) under different underlying conditions.

		Reader 2				
A		H	W			
Reader 1	H	81	9	90	$\pi_{H\|H} = 0.9$	$P_o = 0.98$
	W	9	901	910	$\pi_{W\|W} = 1.0$	$\kappa = 0.89$
	Total	90	910	1000	$p = 0.1$	
B		Reader 2				
		H	W			
Reader 1	H	25	25	50	$\pi_{H\|H} = 0.5$	$P_o = 0.95$
	W	25	925	950	$\pi_{W\|W} = 1.0$	$\kappa = 0.47$
	Total	50	950	1000	$p = 0.1$	
C		Reader 2				
		H	W			
Reader 1	H	410	90	500	$\pi_{H\|H} = 0.9$	$P_o = 0.82$
	W	90	410	500	$\pi_{W\|W} = 0.9$	$\kappa = 0.64$
	Total	500	500	1000	$p = 0.5$	
D		Reader 2				
		H	W			
Reader 1	H	50	90	140	$\pi_{H\|H} = 0.9$	$P_o = 0.82$
	W	90	770	860	$\pi_{W\|W} = 0.9$	$\kappa = 0.25$
	Total	140	860	1000	$p = 0.05$	

ditional latent classes may be added (Christensen et al., 1992; Formann, 1994), e.g. a third class of otoliths from ambiguous sources.

In the previous discussion concerning three or more readers, we implied that readers were different individuals. This need not be so; what is required are three or more independent readings. If it were possible for the same individual to read the same otolith more than once, independently, then the number of different readers could be reduced. If independence could not be met, the dependence could be modeled, as discussed above.

Another critical assumption, but one that should be met most of the time, is that the individual accuracy rates are known to be either greater than or less than the error rates (e.g. $\pi_{H|H} > \pi_{W|H}$ and $\pi_{W|W} > \pi_{H|W}$, which implies that $\pi_{H|H}$ and $\pi_{W|W}$ are either greater than or less than 0.5) because of an inherent symmetry in the problem that results in the same likelihood function being generated when the error rates are switched with the accuracy rates.

Computation Formulas for estimating κ and its standard error are straightforward (Fleiss, 1981). Estimates can also be obtained from several software packages including PROC FREQ in SAS (SAS Institute, 1989).

Maximizing either of the likelihood functions for the LCMs requires a numerical procedure. The most straightforward is to use an optimization routine such as "Solver" in Excel (Microsoft Corporation, 1993) or "nlminb" in S-PLUS (Statistical Sciences, 1995). Alternatively, the EM algorithm (Dempster et al., 1977; Dawid and Skene, 1979; McLachlan and Krishnan, 1997) can be easily used. The simplicity of the EM algorithm follows from the recognition that the LCM is an example of a finite mixture problem, specifically, in this case, a mixture of multivariate Bernoulli distributions with mixing parameter p (Everitt, 1984). Use of the EM algorithm for such mixture problems in fisheries is well documented, e.g. for stock composition estimates (Millar, 1987; Pella et al., 1996) and for age-length keys (Kimura and Chikuni, 1987). A more efficient alternative to the EM algorithm is to use iteratively reweighted least squares (Agresti, 1990). This method is relatively easy to implement in software such as PROC NLIN in SAS (SAS Institute, 1989). Perhaps the most direct and efficient way would be to use LCM software. We are not aware of any routines for LCMs in any major statistical package at present, but several independent LCM packages exist (for a review, see Clogg, 1995; and for an Internet listing see http://ourworld.compuserve.com/homepages/jsuebersax/index.htm).

As with many maximum likelihood problems, where numerical methods must be used, complications can arise. Constraints may at times be needed to ensure that parameter estimates fall in acceptable intervals (e.g. [0,1] for p and [0.5,1] for the π's). Also the likelihood function may have local maxima, which means that several runs with varying starting values may be necessary to identify the global maximum. Finally, estimates of standard errors may entail additional computing. PROC NLIN in SAS provides asymptotic (i.e. large-sample) standard errors. Jackknife and bootstrap estimates are relatively easy to program, the jackknife being much less computationally intensive.

Finally, the Bayesian programs discussed in Joseph et al. (1995) can be found at http://www.epi.mcgill.ca/Joseph/software.html.

Examples

The first example analyzes the results of three readers examining 570 chum otoliths. The samples were taken from a common location, and the readers were familiar with the patterns. Each reading was made without knowledge of prior readings. The data, along with pairwise κ estimates and the LCM parameter estimates (using PROC NLIN in SAS; see appendix for code) are presented in Table 3.

These results indicate that the third reader is significantly (α=0.05) less able to correctly identify a hatchery mark when it is present and that there are no significant differences among readers in their ability to detect a wild mark when it is present. These conclusions are readily apparent from the table of results, and although the pairwise κ's are consistent with these results, they are more difficult to interpret. With the variance due to sampling estimated to be $(0.7379)(1 - 0.7379)/(570 - 1) = 0.0003399$, misclassification error contributes only 0.36% to the total variance.

The second example consists of two readers with four spatial strata. Samples were obtained from sockeye salmon caught in four neighboring Alaskan gillnet fisheries in central Southeast Alaska. The data and the LCM estimates are shown in Table 4. These estimates indicate that the readers are not statistically different in their ability to detect hatchery marks, whereas the second reader is better able to distinguish wild marks. With eight parameters and 12 df, there are 4 df available for a goodness-of-fit test. Pearson's chi-square yields 4.83, which with 4 df, has a p-value of 0.306, thus indicating an acceptable model fit. Misclassification error contributes from about 8% to 14% to the total variance in the estimates of the proportion of hatchery stock.

Design considerations

Design of an otolith reading program is complicated by misclassification error. An important consideration is the precision of the estimates, in particular the precision of the estimate of p. Table 5 shows the asymptotic standard error of $\hat{p}$ for various combinations of p, $\pi_{H|H}$, and $\pi_{W|W}$ for the three-reader model with unknown accuracies, and the one-, two-, and three-reader models with accuracies assumed known. Although this table is derived for a sample of 1000 otoliths, the ratio of any two standard errors within the table would be the same for any sample size (assuming the sample size is large enough to approximate the asymptotic conditions). It is evident that misclassification inflates the standard error over the usual binomial case (right-most column). The table also makes clear the increase in the uncertainty of estimating p when the accuracies also have

Table 3

Cross-classification data and results for 570 chum otoliths examined by three readers showing the parameter estimates and standard errors from the latent class model, followed by a comparison of the differences among reader pairs by using kappa and the latent class model (LCM) accuracy rates. The data show that the high agreement among readers as to hatchery and wild classification (e.g. HHH=406 and WWW=135) is reflected in the overall high accuracy rates estimated from the LCM. However the model also shows that reader 3 has a significantly lower accuracy rate in detecting hatchery marks ($\pi^{(3)}_{H|H}$=0.969) than the other readers.

Reading	Count	LCM Parameter	Estimate	SE
HHH	406	$\pi^{(1)}_{H\|H}$	0.998	0.002
HHW	13	$\pi^{(2)}_{H\|H}$	0.998	0.002
HWH	1	$\pi^{(3)}_{H\|H}$	0.969	0.008
WHH	1	$\pi^{(1)}_{W\|W}$	0.958	0.017
HWW	6	$\pi^{(2)}_{W\|W}$	0.986	0.010
WHW	2	$\pi^{(3)}_{W\|W}$	0.957	0.017
WWH	6	p	0.738	0.018
WWW	135			

Reader pairs	κ	SE	Difference in $\pi_{H\|H}$	SE	Difference in $\pi_{W\|W}$	SE
1 and 2	0.954	0.014	0.000	0.004	–0.028	0.020
1 and 3	0.882	0.022	0.029	0.009	0.000	0.024
2 and 3	0.901	0.021	0.029	0.009	0.028	0.020

Table 4

Cross-classification data for 2340 sockeye otoliths examined by two readers and stratified by four fishing districts, showing the estimates of the latent class parameters and their standard errors. Between-reader comparison is based on whether the difference in accuracy estimates are significantly different than zero. The results indicate that the readers were not statistically different in detecting hatchery marks ($\pi_{H|H}$) but were statistically different in detecting wild marks ($\pi_{W|W}$). LCM = latent class model.

	Fishing districts			
	108–30	108–50	106–41	106–30
HH	152	127	85	20
HW	11	9	21	5
WH	2	6	5	1
WW	271	382	832	411
n	436	524	943	437

LCM parameter	Estimate	SE	Reader difference	SE
$\pi_{H\|H}{}^{(1)}$	0.980	0.013	0.017	0.025
$\pi_{H\|H}{}^{(2)}$	0.964	0.021		
$\pi_{W\|W}{}^{(1)}$	0.984	0.005	–0.013	0.006
$\pi_{W\|W}{}^{(2)}$	0.997	0.003		
$p_{108–30}$	0.366	0.024		
$p_{108–50}$	0.257	0.020		
$p_{106–41}$	0.096	0.010		
$p_{106–30}$	0.047	0.011		

to be estimated in the three-reader case. For example, if $\pi_{H|H} = \pi_{W|W} = 0.8$ for all three readers, one would have to have almost twice (0.035/.019=1.84) the sample size to estimate a p of about 0.5. Once accuracy estimates for the readers are obtained, dropping one or even two readers may be appropriate, although the assumption must be made that the accuracy rates will be constant for the remainder of the program. Maintaining two readers will allow for that

Table 5

Asymptotic standard errors for the estimated proportion of marked fish, $\hat{p}$, for various combinations of accuracy rates in identifying hatchery fish, $\pi_{H|H}$, and wild fish, $\pi_{W|W}$, and mark proportion p, for a sample of 1000 otoliths. Values are reported for the cases where accuracy rates, π, are the same and assumed known for one, two, or three readers, and for the case where π's are estimated for three readers. Table illustrates how misclassification will increase standard errors in the estimate of hatchery proportion.

	$\pi_{H\|H}$	0.8			0.9			1.0		
	$\pi_{W\|W}$	0.8	0.9	1.0	0.8	0.9	1.0	0.8	0.9	1.0
	p									
3 readers	0.1	0.032	0.016	0.011	0.023	0.013	0.010	0.018	0.011	0.009
(π's estimated)	0.3	0.034	0.021	0.017	0.024	0.017	0.015	0.020	0.015	0.014
	0.5	0.035	0.023	0.019	0.023	0.018	0.016	0.019	0.016	0.016
	0.7	0.034	0.024	0.020	0.021	0.017	0.015	0.017	0.015	0.014
	0.9	0.032	0.023	0.018	0.016	0.013	0.011	0.011	0.010	0.009
3 readers	0.1	0.013	0.011	0.010	0.011	0.010	0.009	0.010	0.010	0.009
(π's known)	0.3	0.018	0.016	0.015	0.017	0.015	0.015	0.015	0.015	0.014
	0.5	0.019	0.018	0.016	0.018	0.017	0.016	0.016	0.016	0.016
	0.7	0.018	0.017	0.015	0.016	0.015	0.015	0.015	0.015	0.014
	0.9	0.013	0.011	0.010	0.011	0.010	0.010	0.010	0.009	0.009
2 readers	0.1	0.015	0.013	0.010	0.013	0.011	0.010	0.011	0.010	0.009
(π's known)	0.3	0.020	0.018	0.015	0.018	0.016	0.015	0.015	0.015	0.014
	0.5	0.022	0.019	0.016	0.019	0.018	0.016	0.016	0.016	0.016
	0.7	0.020	0.018	0.015	0.018	0.016	0.015	0.015	0.015	0.014
	0.9	0.015	0.013	0.011	0.013	0.011	0.010	0.010	0.010	0.009
1 reader	0.1	0.023	0.017	0.011	0.020	0.015	0.010	0.018	0.014	0.009
(π's known)	0.3	0.026	0.021	0.017	0.022	0.019	0.016	0.020	0.017	0.014
	0.5	0.026	0.022	0.019	0.022	0.020	0.017	0.019	0.017	0.016
	0.7	0.026	0.022	0.020	0.021	0.019	0.017	0.017	0.016	0.014
	0.9	0.023	0.020	0.018	0.017	0.015	0.014	0.011	0.010	0.009

assumption to be checked because there will now be extra degrees of freedom to assess goodness-of-fit (there are 3 df, but only one parameter, p, needs to be estimated). Estimates of p can still be obtained with one reader, but there can be no check of the assumptions. Also, there can be a significant increase in uncertainty in the estimate in using only one reader.

Discussion

There are numerous classification problems in fisheries that require the judgment of trained individuals. In many of those situations no "gold standard" is available to test those judgments, and it becomes necessary to apply other methods to determine the veracity of the classifications. Reading thermally marked otoliths is a particularly good example of this problem because thousands of classification decisions are needed each year to provide estimates of hatchery contributions.

The common approach for assessing the quality of the readings, in the absence of having samples of known origin, has been to collect independent and multiple readings on the samples, and to presume that agreement between readings can serve as a proxy for reading accuracy. Agreement indices such as κ are very easy to compute, and they have utility in that they can serve as flags to indicate reading problems. However, as was shown here, they also suffer difficulties in interpretation. Also, the indices in themselves do not provide inferences about the relative skill of different readers in pulling out a particular set of patterns.

Latent class models provide an approach with readily interpretable quantities for a modest computational cost. Classification accuracies or errors are direct, meaningful parameters unlike an index of agreement. In addition, estimates of p are available. These models can be readily extended to the case of more than two outcomes, e.g. multiple hatchery marks. These models could also be useful in other applications, such as in aging fish or in the identification of any character for which there is no "gold standard" (e.g. field identification of species or sex). A somewhat similar analysis has been proposed for aging (Richards et al., 1992), although the link to LCMs was not discussed. LCMs can handle fairly complicated situations, including ordered classes (Croon, 1990), continuous manifest variables, and parameter constraints (see Clogg, 1995, and Krzanowski and Marriott, 1995, for reviews).

We have not discussed the Bayesian approach to these problems in great detail, but we believe it has much to offer in that it can incorporate prior information, either

in the form of expert opinion (e.g. Demissie et al., 1998) or in the form of results of earlier analyses (e.g. Viana et al., 1993). Rather than assuming that estimated accuracies are "known," one can incorporate the uncertainty in the estimates into the prior distributions. In addition, the Bayesian approach does not rely on asymptotic results that may behave poorly with small samples. We have also not assessed the possible bias due to the lack of independence in the readings. When suitable software becomes available, this assumption should be checked.

In our examples above, misclassification error contributed relatively little to the overall uncertainty. In these applications, where estimates of hatchery contribution were used to make management decisions, the accuracy of readings were within an acceptable range. However, the criteria used to establish quality control standards in any program need to be developed in the context of how the information is to be used along with other sources of uncertainty.

In conclusion, we believe that the use of agreement measures in combination with latent class models can contribute significant information about both the proportions of interest and the quality control aspects of an otolith-marking program. Furthermore these approaches could have application to similar areas in fisheries which require judgments that are not free of error.

Acknowledgments

We thank Bob Wilbur for editorial comments and three anonymous reviewers for valuable suggestions.

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Appendix

The following SAS (version 6.12) code was used to estimate parameters in the three-reader model discussed above. This program makes use of iteratively reweighted least squares to maximize the likelihood function. Observed values (e.g. the number of HHH) are equated with the corresponding expected value from the model and a weighted least squares fit is computed by using PROC NLIN. This computation is iterated to convergence of the parameter estimates. Weights are inverses of the predicted values at each iteration. Indicator variables for each possible outcome are generated so that a model in typical regression form can be written. Bounds on the parameter estimates may be needed to constrain the estimates to the appropriate intervals. Note that the asymptotic standard errors provided by SAS will be correct if the option SIGSQ=1 is specified. However, the printed degrees of freedom and the associated confidence intervals are not correct for this application. The residual weighted sum of squares listed by SAS is the chi-squared goodness-of-fit-statistic. The option, OUTEST, outputs point estimates and the the estimated covariance matrix for the parameters. SAS code for the multistrata model used in the second example is also available from the authors.

```
/* SAS Code for estimating 3-reader, 1-stratum model */

data a;
  array x{8} x1-x8;
  input y;
  ntot+y;                                  /* accumulating sample size */
  if _n_=8 then call symput('ntot',ntot);  /* put total into macro var */
  do i=1 to 8;
    if i=_n_ then x{i}=1; else x{i}=0;     /* set up indicator variables */
  end;
  cards;
 406      /* H H H */
  13      /* H H W */
   1      /* H W H */
   1      /* W H H */
   6      /* H W W */
   2      /* W H W */
   6      /* W W H */
 135      /* W W W */
;

proc nlin data=a nohalve sigsq=1 outest=est;          /* sigsq=1 for correct se's */
  parms a1=.9 a2=.9 a3=.9 b1=.9 b2=.9 b3=.9 p=.6;     /* starting values */
  e1=a1*a2*a3*p+(1-b1)*(1-b2)*(1-b3)*(1-p);           /* a is accuracy for H */
  e2=a1*a2*(1-a3)*p+(1-b1)*(1-b2)*b3*(1-p);           /* b is accuracy for W */
  e3=a1*(1-a2)*a3*p+(1-b1)*b2*(1-b3)*(1-p);
  e4=(1-a1)*a2*a3*p+b1*(1-b2)*(1-b3)*(1-p);
  e5=a1*(1-a2)*(1-a3)*p+(1-b1)*b2*b3*(1-p);
  e6=(1-a1)*a2*(1-a3)*p+b1*(1-b2)*b3*(1-p);
  e7=(1-a1)*(1-a2)*a3*p+b1*b2*(1-b3)*(1-p);
  e8=(1-a1)*(1-a2)*(1-a3)*p+b1*b2*b3*(1-p);
  model y=(e1*x1+e2*x2+e3*x3+e4*x4+e5*x5+e6*x6+e7*x7+e8*x8)*&ntot;
  bounds  0.5<=a1<=1, 0.5<=a2<=1, 0.5<=a3<=1, 0.5<=b1<=1, 0.5<=b2<=1,
          0.5<=b3<=1, 0<=p<=1;
  _weight_=1/model.y;
run;
```

Abstract—Distribution, abundance, and several population features were studied in Ensenada de La Vela (Venezuela) between 1993 and 1998 as a first step in the assessment of local fisheries of swimming crabs. *Arenaeus cribrarius* was the most abundant species at the marine foreshore. *Callinectes danae* prevailed at the estuarine location. *Callinectes bocourti* was the most abundant species at the offshore. Abundances of *A. cribrarius* and *C. danae* fluctuated widely and randomly. Ovigerous females were almost absent. Adults of several species were smaller than previously reported. This study suggests that fisheries based on these swimming crabs probably will be restricted to an artisanal level because abundances appear too low to support industrial exploitation.

Local distribution and abundance of swimming crabs (*Callinectes* spp. and *Arenaeus cribrarius*) on a tropical arid beach

Carlos A. Carmona-Suárez
Jesús E. Conde
Centro de Ecología, Instituto Venezolano de Investigaciones Científicas
A.P. 21827
Caracas 1020-A, Venezuela
E-mail address (for C. A. Carmona-Suárez): ccarmona@oikos.ivic.ve.

Swimming crabs of the family Portunidae are common in coastal habitats in tropical, subtropical, and temperate regions. Species of the genus *Callinectes* are widely distributed in the neotropics and subtropics (Norse, 1977; Williams, 1984) where they are a key resource in local fisheries (Ferrer-Montaño, 1997; Fischer, 1978; Oesterling and Petrocci, 1995) and are important in trophic relations of fish and organisms of sandy and sandy-mud bottoms (Arnold, 1984; Lin, 1991), and in seagrass meadows (Orth and van Montfrans, 1987; Wilson et al., 1987). Several species of portunids have been thoroughly studied (e.g. *C. sapidus*), and many aspects of their biology, ecology, biogeography, and fisheries (including types of fisheries and the commercial exploitation of these species as "soft-shell" crabs) have been addressed, (Taissoun, 1969, 1973a, 1973b; Norse, 1977, 1978; Norse and Estevez, 1977; Perry and Van Engel, 1979; Williams, 1984; Smith et al., 1990). However, some species remain poorly known. Knowledge about species of *Callinectes* is mainly restricted to temperate regions, in spite of their commercial importance in the Caribbean. Furthermore, although several features of the speckled swimming crab, *Arenaeus cribrarius*, have been studied in Brazil, such as relative growth and some ecological aspects of populations (Avila and Branco, 1996; Pinheiro et al., 1996, 1997; Pinheiro and Fransozo, 1993, 1998, 1999), and elsewhere, such as its role in the trophic web in a sandy beach in South Carolina and its larval development (Stuck and Truesdale, 1988; DeLancey, 1989), as far as we know there are no published accounts of its abundance in the southern Caribbean.

Several studies of portunids have been conducted on Venezuelan coasts (Taissoun, 1969, 1973a, 1973b; Rodríguez, 1980; Scelzo and Varela, 1988; Carmona-Suárez and Conde, 1996), including species that are commercially important at an industrial level and as a mainstay for artisanal and subsistence fisheries in many coastal villages (Ferrer-Montaño, 1997; Conde and Rodríguez, 1999). A few studies with emphasis on biogeographical, taxonomic, and morphometric features of the family have been conducted in Lake Maracaibo, a polyhaline system (Taissoun 1969, 1972, 1973a, 1973b; Schubart et al., 2001). Seven species of *Callinectes* and the speckled swimming crab, *A. cribrarius*, have been listed for the State of Falcón (Carmona-Suárez and Conde, 1996), which is characterized by protracted desolate coasts, sandy and sand-mud beaches (Carmona and Conde, 1989), and an abnormally arid climate (Lahey, 1973). Lake Maracaibo, which is roughly 240 km west of Ensenada de La Vela, has the largest crab and crabmeat industry in Venezuela. Most of it is exported to the United States, where it accumulated a total value of US$ 6.2 million in 1992 (Oesterling and Petrocci, 1995). The main crab species captured in this area is *C. sapidus*. Crabs have also been harvested near Punto Fijo and Coro, the latter just 10 km from Ensenada de La Vela. In this locality, *C. bocourti* is harvested by artisanal fishermen (senior author, personal obs.). In spite of this, nothing is known about the abundance, microdistribution, and population traits of

Manuscript accepted 16 February 2001.
Fish. Bull. 100:11–25 (2002).

swimming crabs on these arid beaches. Our study is thus important both ecologically and as a preliminary assessment of stock levels and their potential for sustainable exploitation. Also, few studies address the guild structure of portunid crabs in the Caribbean Basin (Taissoun, 1969, 1973a; Moncada and Gómez 1980; Buchanan and Stoner 1988), in spite of their importance to fisheries.

The purpose of our study was to widen our knowledge of the population biology of *A. cribrarius* and various species of *Callinectes* in the Southern Caribbean. We quantified the distribution and population aspects of several species of *Callinectes* and *A. cribarius* on a sandy beach and in a small estuary located on an arid shoreline in Falcón, western Venezuela. We present data on the distribution and abundance of a guild of portunids, their physical correlates, and some population characteristics of the dominant species in marine and estuarine habitats.

Materials and methods

Sampling area

Ensenada de La Vela (11°27′N, 69°34′W) is a small cove located on the central coast of the State of Falcón in western Venezuela next to Istmo de Médanos, a narrow low-lying isthmus that links Península de Paraguaná to the mainland (Fig. 1). Ensenada de La Vela lies at the center of a region that extends from eastern Panamá to the Paria Peninsula in eastern Venezuela that has been regarded as abnormally dry (Lahey, 1973). In Falcon's western coastal strip and in the Península de Paraguaná, rainfall is scarce and seasonal with peaks during October–December, when nearly 50–60% of the precipitation occurs. The average yearly rainfall on the peninsula is 400 to 600 mm (Goddard and Picard, 1976), although in some localities the environment is harsher with a mean of 256.8 mm (Conde and Díaz, 1992b). The mean air temperature is 27.7°C, and the average wind speed is 10 kph and seasonal (Goddard and Picard, 1976). No mangroves, coral reefs, or seagrass beds appear at Ensenada de La Vela.

Sampling procedures

All samplings were carried out outside the fishing areas used by local fishermen. Our study was conducted in three stages. During the first and second stages, crabs were sampled at two major biotopes, where three open-water marine stations at the foreshore and one enclosed estuarine station were set. Station 1 was located on the eastern corner of Ensenada de La Vela, the most protected area, where the surf action is extremely weak. Station 2 was also located in the marine front, but next to the inlet of a natural estuarine impoundment where a nearby basin drains. Station 3 was established in this estuarine area, which is not freely connected to the ocean because its exchange mouth is blocked by a sandbar for most of the year. Station 4 was also set at the oceanic front, but in a zone exposed to rugged surf, next to an area that has the strongest wave action in Venezuela. Marine stations were characterized by sandy bottoms, low-transparency waters, and low-lying coastal profiles, whereas the estuarine station was mainly composed of muddy substrate, and had little water movement. Most of the bottom was devoid of vegetation and was interspersed with scarce flat rocky patches. As a whole, some 300 m of shoreline were trawled during each sampling.

During the first stage of sampling, trawling and environmental measurements were conducted monthly at each station from January 1993 to December 1994. Field campaigns included both rainy and dry seasons. Crabs were collected using a 7-meter long and 1.5-m tall hand seine (locally known as a "chinchorro"), with a mesh diameter of 1.0 cm. The hand seine was trawled perpendicular to the coast by two persons walking alongside the net in a 20-m long strip, parallel to the coast, at a depth ranging from 1 to 1.5 m. We repeated this process four times consecutively at approximately the same site. This is the procedure that local fishermen use to capture shrimp and fish to optimize fishing effort. Because waves break and depth does not exceed 1.5 m at our sampling sites, these sites were unsuitable for the other types of fishing gear used in other studies for capture of swimming crabs, such as crab pots, trot lines, otter trawls, and dip nets, among others (Sholar, 1979; van Montfrans et al., 1986; Prager et al., 1990; Ryer et al., 1990; Hsueh et al., 1992). Our method was also used by Carmona-Suárez and Conde (1996) to inventory brachyuran crabs in the State of Falcón, Venezuela. After each trawl at a given station, captured crabs were put in a bucket until sampling at that specific site was completed. When all four trawls were completed and the data were recorded, crabs were returned alive to the same place.

Because the behavior of some swimming crabs has been hypothesized to follow daily cycles of burrowing in the substratum during the day and of emerging at night (Warner, 1977; Fischer, 1978), we conducted a second stage of samplings from September 1997 to February 1998 at the same sites. We sampled during the day and the night of the same day or on consecutive days to determine if there were any systematic differences in the composition of the guild, in the abundance, size, and sex ratios of crabs, and to detect potential biases introduced by the sample design used in stage 1. The gear and sampling design for stage 2 was the same used during stage 1, but we were unable to collect crabs at the estuarine station because of a discharge of untreated domestic sewage at the beginning of 1997.

The purpose of the third sampling stage was to assess if guild composition and other characteristics were influenced by depth or by distance from the coast. Three new stations (inshore, midshore, and offshore) were sampled simultaneously in August 1998 and from June to July 1999, from the foreshore oceanward at intervals of 50 m (Fig. 1). The depth at the inshore station was ~1.5 m, and the depths at the mid- and offshore stations were ~2.5–3 m. During this stage, two crab pots with fish bait (as described by Oesterling, 1984) were deployed at each station for approximately 12 hours during the day, and for the same amount of time during the night, except in August 1998, when pots were deployed for 6 hours during the day and

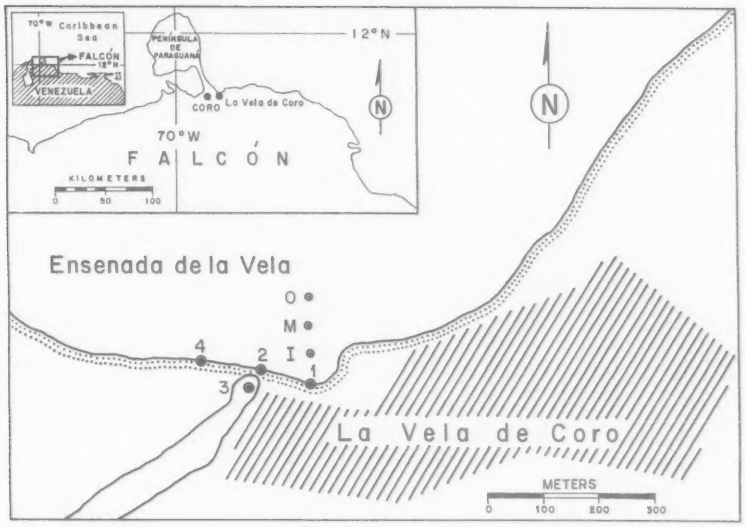

Figure 1

Map of sampling sites at Ensenada de La Vela, State of Falcón, Venezuela. Stations 1 to 4: = foreshore sampling sites (stages 1 + 2); I = inshore sampling site, M = midshore sampling site, O = offshore sampling site (stage 3).

other 6 hours during the night. This process was carried out for three to four consecutive days. No monthly or seasonal samples were taken at these three offshore stations.

Crab identification and characterization

Crabs from each stage were sorted to species, their sex was determined, and each crab was measured immediately after capture. Carapace length was measured with a 0.5-mm-precision Vernier caliper. This measurement was selected instead of carapace width because lateral spines can be abraded, making this measure of body size unreliable. This measurement method has also been used by Moncada and Gómez (1980) and Williams (1984). Animals were identified by using a key compiled from the information and keys in Taissoun (1969, 1973b), Fischer (1978), Rodríguez (1980), and Williams (1984). Juvenile females are identified by a triangular pleon and adults by a semicircular pleon. Adult males have an abdomen detached from the sternum; juveniles do not.

Environmental variables and data analysis

At each station, from January 1993 to December 1994, surface water temperature and salinity were measured with a 0.5°C precision mercury thermometer and a temperature-compensated hand refractometer, respectively. Dissolved oxygen was determined from November 1993 up to December 1994 with a YSI® dissolved oxygen meter. During the second and third sampling stages (1997–98 and 1999) only salinity values were recorded. Rainfall data were retrieved from the raw records of the meteorological station belonging to the Ministry of the Environment and Natural Resources (Venezuela), located at Coro Airport, about 10 km west of the sampling sites.

Population dynamics were analyzed only for the most abundant species that appeared regularly during each sample. Dissimilarities in body size between species were compared by using a two-tailed Student's *t*-test of the differences between two means. Sets of continuous variables were checked for normality with the Kolmogorov-Smirnov goodness-of-fit test. Homogeneity of variances of groups of data to be compared by *t*-tests was checked with Bartlett's test (StatSoft, 1992; Sokal and Rohlf, 1995). In those cases where normality or homoscedasticity were not met, data were log-transformed. Multiple comparisons were performed with the Tukey-Kramer method. The degree of association between crab abundance and environmental variables was assessed with the product-moment correlation coefficient. To compare abundance distributions between stations and diel samplings, R×C tables were analyzed with the *G*-test of independence. No extrinsic hypothesis were considered.

To describe portunid guild composition, several diversity indices were used: Simpson's, Shannon-Weaver, and Hill's numbers (N1 and N2) (Ludwig and Reynolds, 1988). Simpson's index gives the probability that two individuals drawn from a population belong to the same species. The Shannon-Weaver index measures the average degree of uncertainty in predicting to what species an individual chosen at random would belong. Hill's numbers N1 and N2, whose units are number of species, show how many common and very common species appear in a guild or community and lessen the weight of rare species.

Results

Rainfall patterns

In 1993 and 1994, mean annual rainfall at Coro was 228.4 and 58.7 mm, respectively. Precipitation, which was below the historical yearly average (403.5 mm; 1921–87), was distributed irregularly. Wet and dry seasons did not show any evident pattern (Fig. 2). In 1993, rains peaked in April and May, and secondary peaks occurred in July and November, whereas in 1994, precipitation reached a maximum during July–August and there was a lesser amount in January. During the latter year, four months were entirely deprived of rain (Fig. 2).

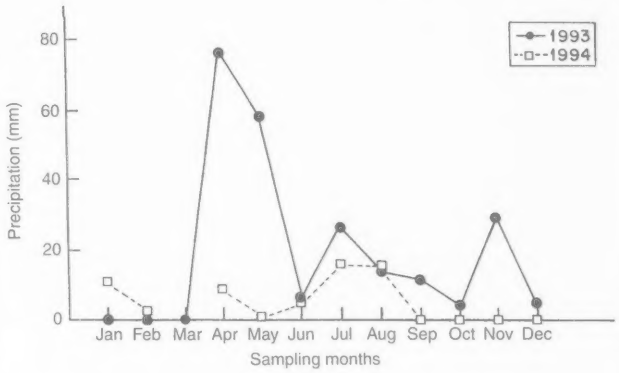

Figure 2
Rainfall in Coro (Falcón, Venezuela) during 1993 and 1994.

Physicochemical variables

Water temperature means and ranges from two-year monthly measurements at the estuarine and three foreshore stations are shown in Figure 3A. Temperature did not differ significantly among marine sites. However, mean water temperature was higher in the estuarine site (Table 1), with an average of 29°C, and so was the range, 25–34°C (Fig. 3A).

Mean salinity and its range varied slightly between marine stations (Fig. 3). The highest value was reached at station 1 and the lowest at stations 1 and 2. Salinity was significantly lower in the estuarine site (Table 1), but its range was much wider than at any other site (Fig. 3). Salinity varied very little over time at the marine stations, with the exceptions of the beginning of 1993, when salinity dropped to nearly 30‰, and November–December 1994 and the onset of 1994, when the water reached hypersaline levels (Fig. 3). Salinity at the estuarine site varied widely through time, peaking in February 1993, January 1994, and August 1994. Minima were registered in September 1993 and July 1994 (Fig. 3).

Mean dissolved oxygen was highest at station 2 and lowest at the estuarine site, where similarly the lowest absolute value observed throughout the study was recorded (Fig. 3). At the marine stations, dissolved oxygen had a smaller range than at the estuarine site, whereas the range was shifted to lower values. Oxygen increased steadily from the end of 1993 until the end of 1994, when concentrations plunged at stations 3 and 4, and less abruptly at station 1. At station 2, the oxygen concentration increased to a maximum value at the end of the year (Fig. 3). However, no significant differences in dissolved oxygen were found between stations (Table 1).

Table 1
One-way ANOVA and Tukey honest significant difference test between three foreshore (stations 1, 2, and 4) and the estuarine station (station 3) in Ensenada de La Vela (1993–94). M = mean.

Temperature: df = 84; F = 4.576; P=0.005*

Stations	1 M=27.418	2 M=27.60	3 M=28.968	4 M=27.532
1		0.982	0.010*	0.995
2	0.982		0.029*	0.999
3	0.010*	0.029*		0.020*
4	0.995	0.999	0.020*	

Salinity: df = 87; F = 47.153; P=0.001*

Stations	1 M=37.409	2 M=36.56	3 M=19.522	4 M=36.391
1		0.966	0.0001*	0.942
2	0.966		0.0001*	0.100
3	0.0001*	0.0001*		0.0001*
4	0.942	0.100	0.0001*	

Dissolved oxygen: df = 52; F = 1.296; P=0.286 not significant

Stations	1 M=7.814	2 M=8.143	3 M=7.021	4 M=7.736
1		0.943	0.535	0.999
2	0.943		0.236	0.899
3	0.535	0.236		0.619
4	0.999	0.899	0.619	

Distribution, abundance and diversity

Surf zone A total of 478 swimming crabs were collected during the first stage of our study in the surf and at the estuarine pond (Table 2). Overall, *A. cribrarius* and *C. danae* dominated. They were followed by *C. bocourti, C. sapidus, C. exasperatus, C. maracaiboensis*, and *C. larvatus*. At the marine biotope, where five species of portunids were caught throughout our study, *A. cribrarius* was the prevailing species, with shares of 77.5%, 73.7% and 86.5%, at stations 1, 2, and 4, respectively. The second most abundant species

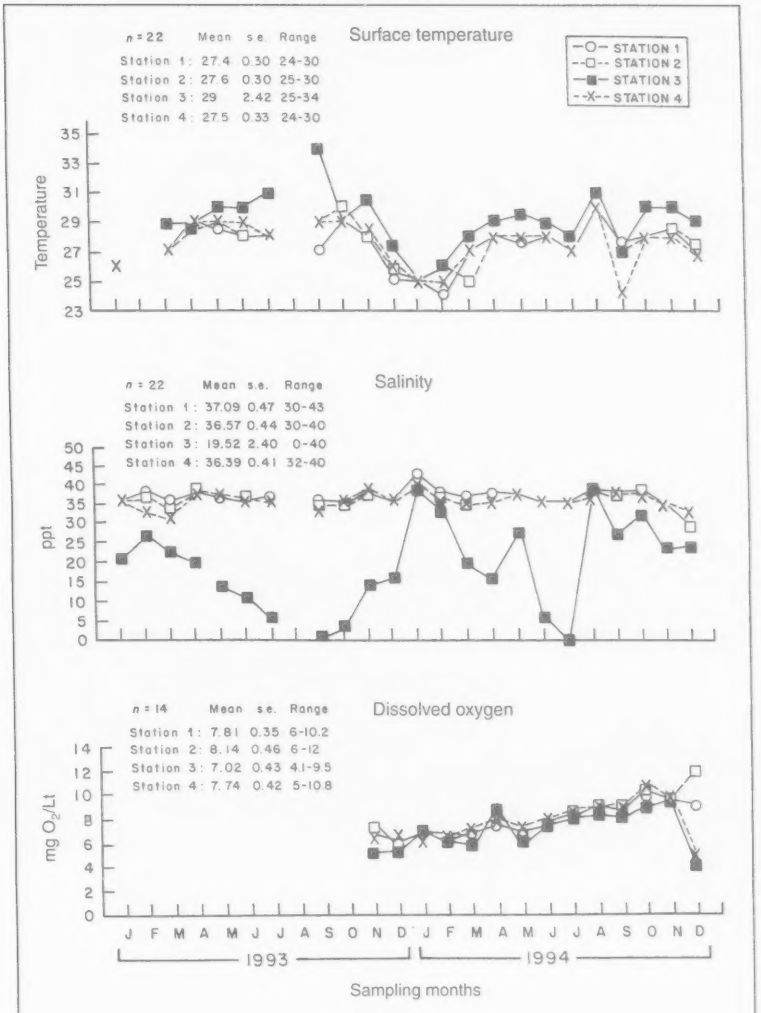
n = 22 Mean s.e. Range
Station 1: 27.4 0.30 24-30
Station 2: 27.6 0.30 25-30
Station 3: 29 2.42 25-34
Station 4: 27.5 0.33 24-30
Surface temperature
STATION 1
STATION 2
STATION 3
STATION 4
Temperature
n = 22 Mean s.e. Range
Station 1: 37.09 0.47 30-43
Station 2: 36.57 0.44 30-40
Station 3: 19.52 2.40 0-40
Station 4: 36.39 0.41 32-40
Salinity
ppt
n = 14 Mean s.e. Range
Station 1: 7.81 0.35 6-10.2
Station 2: 8.14 0.46 6-12
Station 3: 7.02 0.43 4.1-9.5
Station 4: 7.74 0.42 5-10.8
Dissolved oxygen
mg O2/Lt
J F M A M J J A S O N D J F M A M J J A S O N D
1993
1994
Sampling months

Figure 3

Surface temperature, salinity, and dissolved oxygen at the foreshore and estuarine stations in Ensenada de La Vela (Falcón, Venezuela).

at the marine stations was *C. danae* (Table 2). The highest number of species, six, was recorded at the estuarine site, where *C. danae* clearly dominated with a relative abundance of 75.2%, followed by *C. bocourti* (14.1%), *C. exasperatus* (4.5%), *C. sapidus* (2.5%), *C. maracaiboensis* (2.0%) and *C. larvatus* (1.5%). *Arenaeus cribrarius* was absent from the estuarine site. Overall, the highest diversity (Shannon-Weaver index) was registered at the estuarine station, followed by station 2, station 1, and finally station 4, the most exposed tract. Hill's diversity number 1 (N1), which indicates abundant species, was also highest at the estuarine station 3, followed by stations 2, 1, and 4 (Table 2). In a comparison of the two main biotopes (all three marine stations vs. the estuarine station) for the most frequent species (*A. cribrarius* and *C. danae*), their abundance was dependent on salinity (G=306; df=1, P<0.005). However, their abundance was independent of wave exposure, when only the stations in the marine biotope were considered (G=5.624; df=2, 0.05 >P>0.1).

Offshore A total of 173 swimming crabs were caught with crab pots. Abundance was highest at the seaward-most station, followed by the inshore and midshore stations (Table 3). The average number of individuals per pot at each site followed a similar sequence (offshore: 5.9 individuals/pot; inshore: 1.75 ind/pot; midshore: 1.5 ind/pot). Differences in abundance between offshore and inshore and between offshore and midshore stations were

Table 2

Overall abundance (no. of crabs) and diversity indexes for swimming crabs at seaside in Ensenada de La Vela (Venezuela).

		Station 1	Station 2	Station 3	Station 4	Totals (%)
A. cribrarius		86	70	0	64	220 (46)
C. danae		19	22	149	7	197 (41.2)
C. bocourti		0	2	28	1	31 (6.5)
C. maracaiboensis		0	0	4	0	4 (0.8)
C. sapidus		6	1	5	1	13 (2.7)
C. exasperatus		0	0	9	1	10 (2.1)
C. larvatus		0	0	3	0	3 (0.6)
Number of specimens		111	95	198	74	478
Number of species		3	4	6	5	
Simpson (λ')		0.6292	0.5928	0.5876	0.7542	
Shannon-Weaver (H')		0.6580	0.6930	0.8660	0.5230	
Hill's numbers	N1	1.9300	2.0000	2.3780	1.6870	
	N2	1.5894	1.6868	1.7018	1.3260	

Table 3

Overall abundance (no. of crabs) and diversity indexes for swimming crabs captured with crab pots in Ensenada de La Vela (Venezuela).

		Inshore	Midshore	Offshore	Totals
C. bocourti		30	30	69	129
C. maracaiboensis		2	4	13	19
C. danae		3	1	8	12
C. ornatus		6	3	2	11
C. sp. (unidentified)		0	2	0	2
Number of specimens		41	40	92	
Number of species		4	5	4	
Simpson (λ')		0.5537	0.5705	0.5860	
Shannon-Weaver (H')		0.8485	0.8823	0.7879	
Hill's numbers	N1	2.3361	2.4164	2.1987	
	N2	1.8062	1.7528	1.7065	

significant, whereas the difference between inshore and midshore was not. Overall, four species were caught, but *C. bocourti* prevailed at all the stations with at least 73.2% of the total quantity (Table 3). Frequency of crabs by species varied significantly with the distance of the station to the shore (G=17.024, 0.05 >P>0.01, df=8). *C. bocourti* maintained a constant presence through the three stations, ranging from 73.2 to 75.0% of total crabs at each station, the abundance of *C. maracaiboensis* increased seaward, and the abundance of *C. ornatus* decreased. *Callinectes danae* did not show any trend.

In this set of samples, taken at a distance from the shoreline, the highest diversity (Shannon-Weaver index) was registered at the midshore station, closely followed by the inshore station and the offshore station. Hill's diversity number 1 (N1), which indicates abundant species, was also highest at the midshore station, followed by inshore and offshore stations (Table 3).

Temporal variability

Because data for *C. bocourti*, *C. sapidus*, *C. exasperatus*, *C. maracaiboensis* and *C. larvatus* were too scarce to allow useful analysis, temporal variability of the abundance at the surf and at the estuarine pond was examined only for *A. cribrarius*, *C. danae*, and for total crabs. Temporal variability of the abundances of these species are shown in Figure 4. Abundances fluctuated widely and randomly throughout our study. The density of *A. cribrarius* peaked in April, July, and October 1993, as well as in February and October 1994 (Fig. 4). In the estuarine site, *C. danae* abundance peaked in May and October 1993, as well as in February, April, August, and November 1994 (Fig. 4). In the marine sites, *C. danae* abundance was considerably lower and maxima occurred in June, September, and October 1993, and in May and October 1994 (Fig. 4). No significant correlations were found between abundances of these two species and rainfall, water temperature, salinity, and dissolved oxygen (Table 4). However, when total crabs were regressed against rainfall at the estuarine site and oxygen at the foreshore, correlations were significant (Table 4). The negative correlation of this latter factor reached almost significant levels for both species at the marine ecotope.

Diel variations

Surf zone A total of 196 crabs were caught with hand seines at the foreshore during September 1997–February 1998 samplings: 82 crabs at night and 114 during the day (Table 5). Six species appeared in the diurnal samples (*A. cribrarius*, *C. danae*, *C. bocourti*, *C. larvatus*, *C. maracaiboensis* and *C. sapidus*), one of which (*C. sapidus*) did

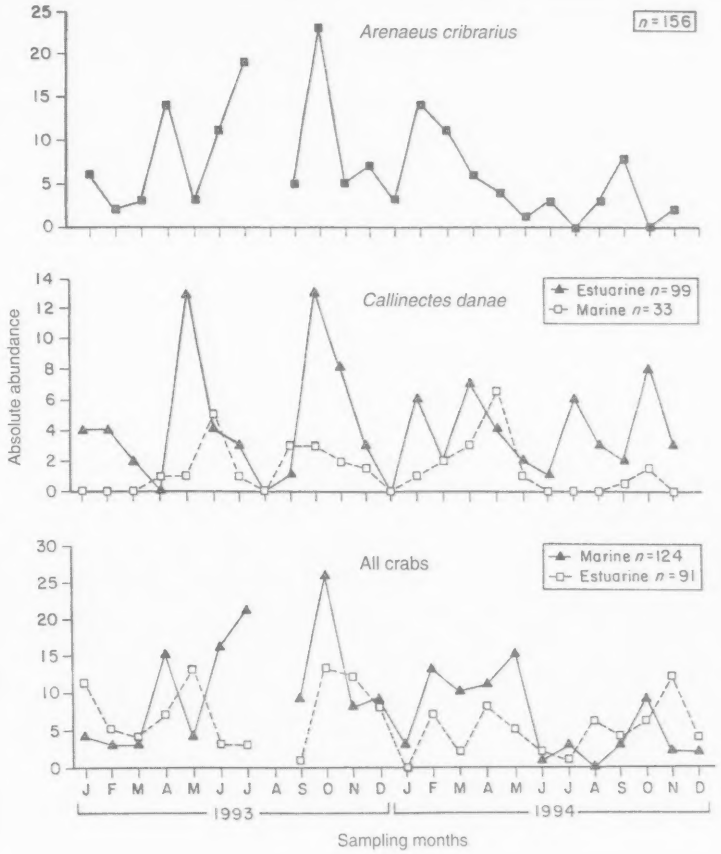

Figure 4

Abundance of *Arenaeus cribrarius*, *Callinectes danae*, and total captured crabs in Ensenada de La Vela (Falcón, Venezuela).

not appear at night. *Arenaeus cribrarius* was the dominant species followed by *C. danae*, during both diurnal and nocturnal samplings, whereas *C. maracaiboensis, C. bocourti, C. larvatus*, and *C. sapidus* were present in very low numbers. Guild composition did not differ significantly between day and night (G=1.630; 0.90>P>0.50; df=5), nor did the average number of individuals per trawl (0.86 vs. 0.62; t=1.702; 0.10>P>0.05; df=262). In both dominant species, *A. cribrarius* and *C. danae*, the average size of crabs caught during daylight hours (Table 5) did not differ significantly from those collected at night, nor did the size frequency distributions (G=3.820; df=4; 0.50>P>0.10). Sex ratios of these two species did not show significant diel differences either (G=0.030; 0.90>P>0.50; df=1; G=2.750; 0.50>P>0.10; df=1, respectively).

Offshore A total of 64 crab pots were deployed, 32 during each period. Four species were caught during both day and night (*C. bocourti, C. maracaiboensis, C. ornatus*, and *C. danae*). A total of 89 crabs were caught during the day and 84 at night (Table 6). *Callinectes bocourti* comprised 73.8% and 75.3% of the abundance during the day and night, respectively, followed by *C. maracaiboensis* (15.5% and 6.7%). No differences in guild composition or sex ratios were found between day and night samples at each of the sites (Table 6). Crab species did not show differences in carapace length between day and night captures (*C. bocourti*, t=0.704, P>0.05, df=155; *C. maracaiboensis*, t=1.355, P>0.05, df=13; *C. ornatus*, t=0.881, P>0.05, df=9; *C. danae*, t=1.811, P>0.05, df=10). Kolmogorov-Smirnov tests run for normality of carapace length distribution for species at the offshore station compared between day and night samples, were statistically nonsignificant.

Sex ratios and ovigerous females

At the foreshore, all the species had male-biased overall sex ratios (Table 7), although only *A. cribrarius*, *C. danae*

Table 4

Correlations between crab abundances and rainfall, salinity, temperature, and dissolved oxygen variables. ns = not significant.

Species	Biotope	Rainfall			Salinity			Temperature			Oxygen		
		r	*n*	Significance	*r*	*n*	Significance	*r*	*n*	Significance	*r*	*n*	Significance
Total crabs	Marine	0.1389	25	ns	–0.0634	34	ns	0.0634	33	ns	–0.4538	25	0.05>*P*>0.01
	Estuarine	0.4028	25	0.05>*P*>0.01	0.0408	34	ns	0.0774	33	ns	0.0620	25	ns
Callinectes danae	Marine	–0.0904	25	ns	0.0107	34	ns	0.1786	33	ns	–0.3155	25	ns
	Estuarine	0.1336	25	ns	0.0231	34	ns	0.2278	33	ns	0.1653	25	ns
Arenaeus cribrarius	Marine	–0.0904	25	ns	–0.0624	34	ns	0.0321	33	ns	–0.3389	25	ns
	Estuarine	----------			----------		Absent	----------			----------		

and *C. sapidus* deviated significantly from the normal Mendelian ratio. Sex ratios for *C. bocourti* and *C. exasperatus* did not differ significantly from equality, possibly because of low sampling numbers for these species. In the estuarine site, none of the sex ratios deviated significantly from an even proportion, although *C. danae* did show a slight bias toward males (Table 7).

No berried females appeared at the foreshore nor at offshore stations. Only two ovigerous females were caught during our study; both were *C. danae* and were collected at the estuarine site in March 1994 (CL [carapace length]: 32.4 mm), and in May 1994 (CL: 43.25 mm).

Body size

Table 8 shows the carapace length (mm) of the most abundant crab species at the foreshore and estuarine stations in Ensenada de La Vela. *Callinectes danae* from the foreshore stations were larger than those from the estuarine site (t=3.799, P<0.05, df=185). The mean cephalothorax length in this species from the foreshore stations was 29.75 mm, whereas in the estuarine zone, crabs averaged 25.16 mm. The average size of adult females from the estuarine station did not differ significantly from those at the foreshore stations. Adult males from the foreshore stations, however, were significantly larger than those from the estuarine site. Male and females sizes did not differ significantly in the foreshore stations, whereas at the estuarine site females were significantly larger (Table 8). Average carapace length of *A. cribrarius* (n=216) was 20.10 (range: 9.48–56.55; SE: 0.496). Juvenile females were significantly larger than juvenile males (t=5.02; P<0.001; df=148). Body size characteristics of *C. bocourti* are shown in Table 8. No differences in size between adult *C. bocourti* males and females from the estuarine site were found (t=0.187; P>0.5; df=14). All Kolmogorov-Smirnov tests run for normality of carapace length distribution for species that were compared at the foreshore and estuarine stations, were statistically nonsignificant.

Discussion

Of the nine species of *Callinectes* that have been reported for the tropical Western Atlantic (Williams, 1984), seven appeared at the foreshore of Ensenada de La Vela during our study. The species with the widest distributions were *C. danae* and *C. sapidus,* which were the only ones to appear at all the stations by the sea margin. *Callinectes maracaiboensis* and *C. larvatus* had the most restricted distribution, occurring only in the estuarine site, and *C. exasperatus* was present only in the estuary and at one of the marine stations. At the marine foreshore stations, *A. cribrarius* was the dominant species, with a share of 78% of the total catch in this ecotope, whereas *C. danae* (19%) was the second most abundant species. Meanwhile, in the estuarine site, where *A. cribrarius* was absent, *C. danae* was the prevailing species, followed by *C. bocourti*. Overall, the highest diversity was registered at the estuarine station, whereas at the foreshore the highest diversity was recorded in the

Table 5

Body size (carapace length in mm) and species abundance during diel observations at the foreshore of Ensenada de La Vela (1997–98). Percentages are given in parentheses in "Abundance" column.

Species	Period	Abundance	Mean body size	SE
A. cribrarius	day	91 (79.8)	19.14	0.94
	night	59 (72.0)	19.38	1.24
C. danae	day	17 (14.9)	21.92	1.89
	night	16 (19.5)	23.09	2.45
C. bocourti	day	1 (0.9)	21.3	—
	night	2 (2.4)	33.83	11.4
C. maracaiboensis	day	2 (1.8)	47.45	9.10
	night	4 (4.9)	37.28	6.05
C. larvatus	day	2 (1.8)	30.55	2.25
	night	1 (1.2)	15.65	—
C. sapidus	day	1 (0.9)	38.4	—
	night	0	—	—
Total	day	114		
	night	82		

Table 6

Distribution of species abundance (no. of crabs found) at the offshore stations during diel samplings and comparisons of sex ratios (all sites pooled).

		C. bocourti	*C. maracaiboensis*	*C. danae*	*C. ornatus*	*C.* sp.[1]	Totals	*G* (df=4)	Significance
Inshore	night	12	2	1	1	0	16	5.238	0.50>*P*>0.10
	day	18	0	2	5	0	25		
Midshore	night	18	3	0	2	2	25	4.226	0.50>*P*>0.10
	day	12	1	1	1	0	15		
Offshore	night	32	8	1	2	0	43	8.506	0.10>*P*>0.05
	day	37	5	7	0	0	49		
Total	night	62	13	2	5	2	84	7.940	0.10>*P*>0.05
	day	67	6	10	6	0	89		
Overall totals		129	19	12	11	2	173		

Sex ratios	*G*	Significance
C. bocourti	0.01	0.975>*P*>0.9
C. maracaiboensis	0.642	0.5>*P*>0.1
C. danae	0.07	0.9>*P*>0.5
C. ornatus	2.864	0.1>*P*>0.05

[1] Unidentified species.

most protected marine stations (2 and 1) followed by station 4, which is located at the most exposed tract. The values of Hill's diversity number 1 (N1) demonstrated a similar pattern and indicated that the number of abundant species was close to two at stations 2 and 3, slightly above this value at the estuarine station, and below at the most exposed station. Offshore guild composition was substantially different from that at the sea margin, as shown by pot samplings. Although several species were common to the three biotopes, each habitat had a distinctive dominant species: *Arenaeus cribrarius* at the surf zone (stations 1, 2, and 4), *C. danae* (station 3) in the estuarine pond, and *C. bocourti* offshore. Because different sampling gears were used at the sea border and offshore because of practical

reasons, comparisons should be regarded as qualitative. However, artisanal fishermen do harvest *C. bocourti* when using beach seines in the areas next to our crab pot stations (senior author, personal obs.).

Inshore-offshore zonations of species at Ensenada de La Vela diverged from the gradients compiled by Norse and Fox-Norse (1979) for other areas in the Caribbean. In many localities, *C. bocourti, C. sapidus,* and *C. maracaiboensis* (the so-called *bocourti* group) are known to inhabit the waters by the seaside, whereas *C. marginatus* and *C. ornatus* are found at the seawardmost zone, and *C. danae* occupies the intermediate area. However, our patterns of

Table 7

Sex ratios for portunids captured in Ensenada de La Vela (1993–94).

	Male:female	Ratio	*G*	df	Significance
Marine stations					
A. cribrarius	155:61	2.5:1	21.607	1	$P<0.005$
C. danae	34:11	3.1:1	6.272	1	$0.01>P>0.025$
C. bocourti	0:1	0:1	—	—	—
C. sapidus	7:0	7:0	5.232	1	$0.01>P>0.025$
C. exasperatus	1:0	1:0	—	—	—
Estuarine station					
C. danae	79:63	1.3:1	0.900	1	$0.5>P>0.1$
C. bocourti	13:15	0.9:1	0.070	1	$0.9>P>0.5$
C. sapidus	2:3	0.7:1	0.088	1	$0.9>P>0.5$
C. exasperatus	7:2	3.5:1	1.405	1	$0.5>P>0.1$
C. larvatus	2:1	2:1	—	—	—
C. maracaiboensis	2:2	1:1	—	—	—

Table 8

Carapace length (mm) for the most abundant species at the foreshore and estuarine stations in Ensenada de La Vela (Venezuela), and comparison of carapace sizes. ns = not significant.

	Marine stations					Estuarine station			
Callinectes danae	*n*	Mean	Range	SE	*Callinectes danae*	*n*	Mean	Range	SE
Juvenile females	8	24.6	14.92–32.7	2.099	Juvenile females	37	22.6	11.28–35.6	1.069
Adult females	3	39.6	36.58–42.0	1.619	Adult females	26	39.8	31.45–47.4	0.832
Juvenile males	14	19.5	8.5–32.4	2	Juvenile males	43	15.8	7.62–27.4	0.691
Adult males	20	39.1	7.42–56.7	2.869	Adult males	36	23.7	10.4–48.4	1.897
	Marine stations only					Estuarine station only			
Arenaeus cribrarius	*n*	Mean	Range	SE	*Callinectes bocourti*	*n*	Mean	Range	SE
Juvenile females	61	22	11.3–36.94	0.831	Juvenile females	7	23.1	11.8–34.4	3.251
Adult females	----------	No adult females		----------	Adult females	10	41	34–45.1	1.126
Juvenile males	89	17.6	10.25–28.64	0.459	Juvenile males	4	19.6	16.6–23	1.314
Adult males	66	21.8	9.48–56.55	1.213	Adult males	6	41.8	24.4–56.5	5.035

		t	df	Significance
C. danae (all crabs)	foreshore/estuarine	3.799	185	$P<0.05$
C. danae (adult females)	foreshore/estuarine	0.065	27	ns
C. danae (adult males)	foreshore/estuarine	4.653	54	$P<0.001$
C. danae (foreshore stations)	females/males	0.766	43	ns
C. danae (estuarine station)	females/males	6.297	140	$P<0.001$

abundance for *Callinectes* species are similar to another Caribbean locality (Buchanan and Stoner, 1988): Laguna Joyuda (Puerto Rico). All the *Callinectes* spp. recorded in this coastal estuarine lagoon were also present in the estuarine station of Ensenada de La Vela. *Callinectes danae* was the dominant species in both sites, whereas *C. exasperatus* and *C. larvatus* were present in low numbers. *Callinectes maracaiboensis* was very scarce at Ensenada de La Vela, but it was not reported at all in Laguna Joyuda (Buchanan and Stoner, 1988), although Buchanan and Stoner cautioned that specimens of this species might have been misclassified and listed as *C. bocourti*. On the other hand, the high abundance of *A. cribrarius* at the marine front of Ensenada de La Vela differed from that of other studies in the Caribbean and Gulf of Mexico, where this species has been reported in low numbers. For instance, in the SW Gulf of Mexico *A. cribrarius* was less than 1% of the total portunid community (García-Montes et al., 1988). In Laguna de Términos (Mexico), a polyhaline coastal lagoon, four species of *Callinectes* were found in a population survey conducted during a whole year, but no individuals of *Arenaeus* were reported (Román-Contreras, 1986). In the same lagoon, Sánchez and Raz-Guzmán (1997) caught a single individual of *A. cribrarius* out of 986 specimens collected over a 17-year span. The differences probably are probably due to the polyhaline conditions at these settings, thus restricting the viability of *A. cribrarius*. However, in temperate sandy beaches, this species can be very common. On Bogue Banks, in North Carolina, *Arenaeus cribrarius* ranked as the most important brachyuran in a high-wave-energy sandy beach (Leber, 1982). In the surf zone at Folly Beach, South Carolina, *A. cribrarius* was one of the dominant brachyuran crabs during the summer and also a key predator of benthic organisms (DeLancey, 1989). *A. cribrarius* is considered to be well-adapted to marine and slightly hypersaline salinity regimes and to habitats with heavy surf and sand scouring in shallow coastal waters (Fischer, 1978; Williams, 1984). This fact was evident in our study, in which *A. cribrarius* was abundant and clearly constrained to a narrow strip in the surf zone.

Our results suggest the importance of salinity as an excluding axis in the distribution of some species of swimming crabs in the surf and estuarine pond of Ensenada de La Vela. In our study, *A. cribrarius* was present in salinities from 30‰ to 43‰, thus exceeding the upper limits of tolerance commonly reported for this species. The restricted distribution of this species is probably a consequence of its stenohalinity (27.5–36.5‰) (Gunter, 1950; Norse, 1978; Williams, 1984; Pinheiro, 1991; Avila and Branco, 1996), although very occasionally it may show up in estuaries (Williams, 1965) and can tolerate experimental salinities down to 17.25‰ (Norse, 1978). This range indicates that *A. cribrarius* prefers marine or near-marine environments, thus explaining its absence in station 3 (estuarine). In spite of being considered to be well adapted to heavy surf in shallow coastal waters (Fischer, 1978; Williams, 1984), *A. cribrarius* appeared to be abundant in all three foreshore stations, independent of water movement, and was most abundant in the more protected stations 1 and 2. Because the salinity did not show any major differences between foreshore and offshore habitats, other factors are at stake in determining the zonation observed for the other species. One of the main elements to consider is substrate composition (Norse and Fox-Norse, 1979; Pinheiro et al., 1997). Pinheiro et al. (1997) stated that distributional patterns of portunids in Fortaleza Bay (Brazil) are driven mainly by the granulometric composition of the sediments. Substrates at the foreshore and estuarine pond differed from offshore bottoms: at the foreshore the sediment was mainly sand; at the estuarine station a muddy bottom prevailed. At the offshore stations, silt was the main substrate. Hence, this difference could influence the distribution of swimming crabs in Ensenada de La Vela.

Callinectes danae was found in both biotopes at the foreshore but was more abundant at the estuarine site. In the marine stations of the surf zone, *C. danae* appeared more frequently in the most protected areas. The appearance and persistence of this species in both environments probably stems from its euryhalinity. In several Caribbean locations, *C. danae* has been observed dwelling in polyhaline environments (Taissoun, 1969; Norse, 1978; Buchanan and Stoner, 1988). Based on this evidence, it is not surprising to find *C. danae* in the entire range of salinities in Ensenada de La Vela, although it is important to underline that at the estuarine station it appeared when salinity was below the minimum (11‰) reported by Norse (1978). Also, several of the portunid species in the surf zone in Ensenada de La Vela were found in higher salinities than those reported by Norse (1978) in several localities in Jamaica, except *C. maracaiboensis* and *C. larvatus*. The absence of *C. ornatus* at the foreshore stations may be due to reasons other than the sampling method, because the same method was used by Carmona-Suárez and Conde (1996), where specimens of *C. ornatus* were frequently captured at different sites in the State of Falcón, Venezuela, including Ensenada de La Vela.

Total abundance of all swimming crabs both at the surf zone and at the estuarine station fluctuated widely and randomly through the year. This pattern also emerged when only the temporal abundance variations of the dominant species, *A. cribrarius* and *C. danae*, were examined. No significant correlations were found between abundances of these two species and rainfall, dissolved oxygen, water temperature, or salinity fluctuations. However, the inverse correlation of dissolved oxygen and abundance reached almost significant levels for both species at the marine foreshore and indeed was significant for the total abundance of crabs in the surf. Additionally, there was a positive correlation between rainfall and total abundance of crabs in the estuarine zone, possibly due to the increment of organic material washed into this environment from adjacent terrestrial areas. Although bibliographic evidence supports the adaptation of portunids to low levels of dissolved oxygen in their environment (DeFur et al., 1990; Rantin et al., 1996; Mangum, 1997), and the relation between respiration rates and salinity in two *Callinectes* species (Rosas et al., 1989), nothing supports the idea that the increase of swimming crab densities is due to the decrease in dissolved oxygen. It might be possible that augmenting food resources would increase populations of fishes and invertebrates

or planktonic blooms, which in turn would require a higher oxygen demand in the area, subsequently provoking drops in oxygen and causing mortalities of high-oxygen-demanding invertebrates. In any event, these results suggest that fluctuations in oxygen levels might be a key element in regulating portunid populations at Ensenada de La Vela and merit further research efforts.

Berried females were remarkably scarce during our study. Only two, both belonging to *C. danae,* were caught throughout the first period at the estuarine site, and none were caught during day and night samplings in the surf zone nor offshore. Nonetheless, scarcity of ovigerous females of swimming crabs in these coasts is not exceptional. During a 2-year survey of crustaceans along 700 km of Falcón's shoreline, Carmona-Suárez and Conde (1996) caught very few berried females of several of the littoral portunid species. They caught only one berried female of *A. cribrarius* and no ovigerous females of *C. sapidus*, *C. larvatus*, *C. ornatus*, or *C. danae*. However, in estuarine areas, substantial numbers of berried females of *C. bocourti*, *C. maracaiboensis,* and *C. exasperatus* were caught in the tidal zone. The scarcity or sheer absence of egg-bearing females in some species of swimming crabs might be the result of habitat partitioning by sex. Differential distributions by sex have been reported for *C. sapidus* (Williams, 1965; Perry, 1975; Archambault et al., 1990), *C. maracaiboensis* (Norse, 1977), and *C. bocourti* (Taissoun, 1969; Norse, 1978). However, for the dominant species in the surf, *A. cribrarius*, ovigerous females do not seem to be segregated into deeper waters. In southern Brazil, ovigerous females of this species appeared in shallow waters close to the coast (Pinheiro et al., 1996). Similarly, many ovigerous females were collected in very shallow water, at the surf's edge in North Carolina (Williams, 1984). Likewise, for *C. bocourti* and *C. maracaiboensis* egg-bearing females have also been reported in marine shallow waters (Norse, 1977). Furthermore, adult females of most species inhabiting the surf zone at Ensenada de La Vela were observed in this area year-round. Thus, alternative explanations should be considered, such as lack of estuarine habitats or sustained harsh environmental conditions that do not allow energy to be invested in reproduction. For instance, a highly seasonal reproductive pattern, with periods without berried females, has been observed in populations of the mangrove tree crab, *Aratus pisonii,* living in hypersaline lagoons in this area (Conde, 1989); this pattern contrasts with the pattern for populations inhabiting other localities, where these crabs reproduce continuously throughout the year (Conde and Díaz, 1989a; Díaz and Conde, 1989). Also, undergrown or stunted specimens of various species of crustaceans have been reported in this area (Conde and Díaz 1989b, 1992a, 1992b; Carmona, 1992; Carmona-Suárez and Conde, 1996). Thus, it is possible that this arid coast lacks the necessary resources for these crabs to reproduce, except in a few estuarine spots. This hypothesis is also supported by the fact that the body size of several species of swimming crabs collected in our study was smaller than that reported in other locations (Fischer, 1978; Williams, 1984).

The only river near the Ensenada de La Vela is the Coro River, which lies approximately 2 km westwards. Because of current direction (east–west), it cannot influence estuarine conditions to the sampled area. The small estuary in the Ensenada de la Vela could be a possible local nutrient supplier. But its influence is restricted to a few days during the end of each year, when the estuary opens to the sea. The setup of an untreated sewage discharge in the small estuarine basin at the beginning of 1997 could in fact have a long-term impact, but it is possible that various species of swimming crabs may not be affected negatively, because of their capacity to live in polluted areas. Such is the case with *C. bocourti* (Taissoun, 1972; Williams, 1974), and *C. sapidus*, the main species in the Lake Maracaibo crab industry (Oesterling and Petrocci, 1995), where contamination due to several sources (i.e. sewage and oil) has reached high levels (Rodríguez, 2000).

Because trawl studies have shown greater abundances of blue crabs (*C. sapidus*) and, in general, other decapods at night (Wilson et al., 1990), we ran a series of day and night samplings at the marine front over a six-month period and later also undertook diel offshore pot sampling on several occasions. Although Fischer (1978) has stated that *A. cribrarius* burrows into the bottom during the day and emerges at night, we collected *A. cribrarius* in the same range of abundances and sizes during both day and night samplings. Similar results were achieved by DeLancey (1989) in South Carolina, where no significant differences were obtained from samples collected at day and night. Wilson et al. (1990) ascribed the lack of differences in day and night abundances of *C. sapidus* to the use of more effective sampling devices than previously employed. In our study, no major differences were observed in diversity, abundance, body size, or sex ratios for most species, even though two kinds of collecting gears were used; thus, it is feasible to consider that if daily cycles exist in the species, they do not have a significant impact on daily density variations. In turn, these findings may have practical consequences for the decisions regarding sampling schemes to assess fisheries in this area.

The exploitation of swimming crabs at Ensenada de La Vela must be considered only at the artisanal level because of the low abundance of all species treated in our work and their wide and random density fluctuations. In fact, local fisheries are currently limited to the artisanal capture of portunids by hanging nets or hand-driven trawling nets. The most captured species by fishermen is *C. bocourti* (senior author, personal obs.), but *C. danae* is also a promising staple to be harvested because it appears in all three major biotopes (marine inshore, offshore, and estuarine). *Arenaeus cribrarius*, a species commercially exploited in Brazil (Pinheiro and Franzoso, 1998) and regarded to have an excellent flavor (Fischer, 1978), may also be considered a target species because of its great abundance, although its small size may make it less desirable commercially.

Acknowledgments

We heartily thank Sebastián Trómpiz, whose involvement in most of the phases of the project was instrumental to

its completion. We thank Omégar Céspedes, Angel López, and Gregorio Gotopo for occasional assistance during field work. Our gratitude extends to María Rondón Médicci, and Nicanor Cifuentes for their critical reading of the manuscript and for assistance during field work in August 1998, and to Eloy Conde, Eloína de Conde and Enrique Molina for logistical support. Last but not least, we thank Kate Rodríguez-Clark for her help with the English text. This study was supported in part by grants CTI 90-068 from the UNEFM and BTA-08 from CONICIT-BID. This work was partially undertaken while C. Carmona-Suárez was a staff member of the Centro de Investigaciones Marinas (UNEFM).

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Age, growth, and reproduction of permit (*Trachinotus falcatus*) in Florida waters

Roy E. Crabtree
Peter B. Hood
Derke Snodgrass

Florida Marine Research Institute
Florida Fish and Wildlife Conservation Commission
100 Eighth Avenue SE
St. Petersburg, Florida 33701-5095
Present address (for R. E. Crabtree): Division of Marine Fisheries
Florida Fish and Wildlife Conservation Commission
620 Meridian St.
Tallahassee, Florida 32399-1600
E mail address (for R. E. Crabtree): crabtrr@gfc.state.fl.us

Abstract–We examined 536 permit (*Trachinotus falcatus*, 65–916 mm FL) collected from the waters of Florida Keys and from the Tampa Bay area on Florida's Gulf coast to describe their growth and reproduction. Among permit that we sexed, females ranged from 266 to 916 mm in length (mean=617) and males ranged from 274 to 855 mm (mean=601). Ages of 297 permit ranging from 102 to 900 mm FL were estimated from thin-sectioned otoliths (sagittae). The large proportion of otoliths with an annulus on the margin and an otolith from an OTC-injected fish suggested that a single annulus was formed each year during late spring or early summer. Permit reach a maximum age of at least 23 years. Permit grew rapidly until an age of about five years, and then growth slowed considerably. Male and female von Bertalanffy growth models were not significantly different, and the sexes-combined growth model was $FL=753.1(1-e^{-0.348(Age+0.585)})$. Gonad development was seasonal, and spawning occurred during late spring and summer over artificial and natural reefs at depths of 10–30 m. Ovaries that contained oocytes in the final stages of oocyte maturation or postovulatory follicles were found during May–July. We estimated that 50% of the females in the population had reached sexual maturity by 547 mm and an age of 3.1 years and that 50% of the males in the population had reached sexual maturity by 486 mm and an age of 2.3 years. Because Florida regulations restrict the maximum size of permit caught in recreational and commercial fisheries to 20-inch (508-mm), most fish harvested are sexually immature. With the current size selectivity of the fishery, the spawning stock biomass of permit could decrease quickly in response to moderate levels of fishing mortality; thus, the regulations in place in Florida to restrict harvest levels appear to be justified.

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The family Carangidae supports a diverse array of economically important fisheries in tropical and subtropical waters worldwide. In the southeastern United States, many carangid stocks are managed at both the state and Federal level. Recently, the National Marine Fisheries Service determined that the Gulf of Mexico greater amberjack stock is overfished, but the status of most carangid stocks is unknown (Anonymous[1]). For most carangid stocks, no quantitative stock assessments have been completed, in part, because little biological information exists regarding carangid growth rates and reproduction. As a result, the adequacy of current management measures to prevent overfishing of many carangid stocks is unclear.

Permit, *Trachinotus falcatus*, are the basis of an important recreational fishery and a small commercial fishery in Florida. Estimates of Florida recreational landings are unreliable but may exceed 100,000 fish per year (Armstrong et al.[2]). Commercial landings of permit peaked in 1991 at 200,000 pounds and then decreased to 50,000 pounds in 1995 (Armstrong et al.[2]). Current regulations in Florida include a 10-inch (254-mm FL) minimum size limit and a 20-inch (508-mm FL) maximum size limit on both the recreational and commercial harvest. In addition, recreational anglers are permitted daily to take 10 permit per bag of combined permit and Florida pompano (*Trachinotus carolinus*). Many anglers pursuing permit do so with professional guides on a charter vessel. In addition to being popular in South Florida, permit are targeted by numerous fishing tourists and recreational anglers in the Bahamas and at locations throughout the Caribbean. Despite the economic importance of permit in these regions, there are no published reports describing growth, longevity, or length and age at sexual maturity. Such information is needed to evaluate the effects of fishing mortality on permit populations. Previous studies of permit life history by Fields (1962) and Finucane (1969) were based only on an examination of larvae and young-of-the year permit. Our study describes growth, longevity, and the length and age at which fish become sexually mature. In addition, we document spawning of permit in South Florida waters based upon a histological examination of ovaries and seasonal patterns in the abundance of juveniles.

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Methods

Collections

Permit that we examined were collected from the Florida Keys (n=308; between 25°40′N, 80°10′W and 24°30′N, 82°20′W) during 1995–97 and the Tampa Bay area (n=228; 27°40′N, 82°45′W) during 1990–95. Most Florida Keys permit were caught with hook-and-line gear (n=215) or speared (n=58) over artificial and natural reefs in the waters off the lower and middle Keys in depths ranging from 10 to 30 m. Other, usually smaller, permit were captured with gill nets (n=16), seines (n=18), and bottom trawls (n=1) over or near shallow banks adjacent to the Keys. Most of the permit sampled in the Tampa Bay area were small (<400 mm FL) and were captured with seines along sandy beaches; some larger Tampa Bay permit were captured with gill nets (n=53) or trammel nets (n=14).

Standard length (SL), fork length (FL), and total length (TL) were measured to the nearest millimeter (mm) and weight was measured to the nearest gram. Unless otherwise indicated, all lengths reported in our study are fork lengths. Otoliths (sagittae) were removed, rinsed in water, and stored dry until sectioned; they were later weighed to the nearest 0.01 mg. Gonad weight was recorded to the nearest gram (g), and gonad samples were removed from the fish and preserved in 10% buffered formalin; they were later soaked in water for 24 hours and stored in 70% ethanol.

Collections of juvenile permit from sandy beaches off Tampa Bay and the Florida Keys were made with a 21.3 × 1.8-m bag seine (6.4-mm mesh in the wings and 3.2-mm mesh in the bag). Seine hauls were made perpendicular to the beach for distances up to 50 m, depending on water depth. Lengths of up to 50 fish from each sample collection were measured to the nearest millimeter. Near Tampa Bay, we collected fish at the Gulf of Mexico beaches of Treasure Island (November 1992 –October 1994; 27°46′N, 82°46.5′W) and Indian Shores (August 1993–November 1994; 27°50′N, 82°50′W). Sampling at each site consisted of five seine hauls every two weeks. Six sandy beaches were sampled monthly in the Florida Keys from July 1994 to July 1997: Lower Matecumbe Beach (July 1994–April 1996; 24°50.95′N, 80°4415′W), Coco Plum Beach (July 1994–April 1996; 24°43.65′N, 81°00.10′W), Clarence P. Higgs Beach, Key West (July 1994–July 1997; 24°32.79′N, 81°47.26′W), Bahia Honda State Park (October 1994–May 1997; 24°39.81′N, 81°15.44′W), Boca Chica Beach (October 1994–April 1996; 24°33.60′N, 81°41.65′W), and Sugarloaf Beach (January 1995–May 1996; 24°36.57′N, 81°33.49′W).

Age and growth

The left sagitta was usually used for age estimation; however, if the left otolith was broken, lost, or destroyed during processing, the right otolith was substituted. We prepared otoliths for age estimation by embedding them in Spurr, a high-density plastic medium (Secor et al., 1992). A 1-mm to 2-mm-thick transverse section containing the otolith core was cut with a Buehler Isomet low-speed saw with a diamond blade. The section was mounted on a microscope slide with thermoplastic glue (CrystalBond 509 adhesive) and was polished with wet or dry sandpaper (grit sizes ranging from 220–2000) until annuli were visible. Sections were then polished on a Buehler polishing cloth with 0.05-gamma alumina powder to remove scratches. Without knowledge of fish size or capture date and using a compound microscope equipped with transmitted light, two readers independently counted annuli on each otolith twice. If three of the four readings agreed, then this mode was accepted as the annulus count. If three of the four readings did not agree, each reader again counted annuli independently and without knowledge of previous counts. If three of the resulting six readings agreed, then this mode was accepted as the annulus count. If there were not three readings that agreed, the otolith was excluded from further analysis. In six cases, two sets of three readings that were in agreement occurred. For these six otoliths the two sets of readings differed by only one annulus; therefore the mean was accepted as the annulus count.

The percentage of otoliths with an annulus on the edge was then plotted by month so that we could look for a seasonal pattern in annulus formation. We did not attempt to measure marginal increments because the margin of permit otoliths is highly sculptured and easily broken; however, we did believe that we could discern the presence of an annulus on the otolith's edge.

The von Bertalanffy (1957) growth equation $FL_t = L_\infty (1-e^{-K(t-t_0)})$ was fitted to observed age-length data with nonlinear regression procedures. Age was esimated as the annulus count because permit both spawn and form annuli at about the same time of year. Our estimates of length at age include some seasonal growth that occurred after the formation of the final annulus. Length-weight regressions were calculated by linear regression of $\log_{10}$-transformed data.

Sex-specific growth models were compared with an approximate randomization test described by Helser (1996). This test is based on the premise that when the null hypothesis of no sex-specific differences in growth is true, a test statistic derived by random assignment of fish to one of two populations will not be different from that observed between sexes. The test statistic is calculated as the residual sums of squares for the sexes-combined von Bertalanffy growth model minus the residual sums of squares for the two sex-specific models. A probability distribution of the test statistic was generated by a randomization routine with 1000 iterations of the nonlinear models. Only sexed fish were included in the statistical comparison.

Age validation

Permit used in the age-validation experiments were captured in waters off the Florida Keys with hook-and-line gear. After capture, permit were tagged with dart-type tags and injected with Liquamycin LA-200 (200-mg oxytetracycline [OTC]/mL) in the dorsal musculature at a dosage of about 100-mg OTC per kg fish weight. Permit were then held in a 33.5-m-long by 5.5-m-wide by 0.75-m-

deep pond at the Florida Fish and Wildlife Conservation Commission's Keys Marine Laboratory in Long Key. Fish were held at ambient temperatures and were fed frozen shrimp and fish until satiated at least three times a week. Although several permit were injected and held for various periods, only one fish survived long enough to have formed an annulus after the OTC injection. The otolith section from this fish was examined with a compound microscope (40–100×) equipped with ultraviolet light so that the fluorescent OTC mark could be detected.

Reproduction

Histological sections of gonads were prepared and assessed for reproductive state. Gonad samples were prepared for histological examination with a modification of the periodic acid Schiff's (PAS) stain for glycol-methacrylate sections and with Weigert's iron-hematoxylin as a nuclear stain and metanil yellow as a counterstain (Quintero-Hunter et al., 1991).

Developmental stages of oocytes were determined and oocytes were counted from histological preparations at 100× with a compound microscope attached to a digital image-processing system. Four oocyte stages were recognized in permit ovaries: primary growth, cortical alveolar, vitellogenic, and oocytes in the final stages of maturation (Wallace and Selman, 1981). The final stages of oocyte maturation (FOM) included yolk coalescence, germinal vesicle migration, germinal vesicle breakdown, and hydration. We also counted postovulatory follicles (POFs) and PAS-positive melanomacrophage centers (Ravaglia and Maggese, 1995; Crabtree et al., 1997), which were present in many ovaries. When stained with the PAS stain, these PAS-positive structures are brilliant purple. Melanomacrophage centers are thought to be active in degrading atretic oocytes, postovulatory follicles, and residual cells of the spermatogenic cycle (Chan et al., 1967; Ravaglia and Maggese, 1995). The developmental stage of at least 300 oocytes and other structures on each slide was determined and counted in arbitrarily chosen fields, and frequencies were expressed as a percentage of the total count. We counted all oocytes that had at least 50% of their area visible in a field before moving to the next field.

We examined seasonal reproductive patterns by plotting monthly juvenile length frequencies and monthly mean gonadosomatic indices (GSIs). Gonadosomatic indices were calculated for 129 sexually mature female permit ranging in length from 476 to 916 mm and for 122 sexually mature male permit ranging in length from 449 to 855 mm as

$$GSI = (GW / (TW - GW))100,$$

where GW = total gonad weight (g); and
TW = total fish weight (g).

Length and age at sexual maturity

Females were considered sexually mature if vitellogenic oocytes were present or if the histological sections appeared disorganized, highly vascularized, and contained widespread evidence of atresia. We followed the classification of Hunter and Macewicz (1985) in recognizing atresia. Most immature females had small well-organized gonads that contained little evidence of atresia. We interpreted the widespread occurrence of PAS-positive melanomacrophage centers in inactive ovaries as evidence of past gonadal development, and we considered permit with regressed (no vitellogenic oocytes present) ovaries that contained many of these structures to be sexually mature. Males were considered sexually mature if testes contained evidence of ongoing spermatogenesis, residual sperm, or widespread PAS-positive melanomacrophage centers associated with gonadal recrudescence. We estimated the length and age at which 50% of the fish in the population reached sexual maturity by fitting a logistic function to the percentage of fish that were sexually mature and to their respective lengths and ages. Regressions were performed with sex as a categorical effect. If sex was a significant effect, the equations were then reduced to separate sex-specific equations. The inflection point of the logistic curves was used as an estimate of the length or age at which 50% of the population had reached sexual maturity.

Results

Permit that we collected from waters off the Florida Keys ranged from 258 to 916 mm in length (n=308), and the permit collected from the Tampa Bay area ranged from 65 to 812 mm in length (n=228). Among permit that we sexed, females ranged from 266 to 916 mm in length (mean=617, SD=155.7, n=187) and males ranged from 274 to 855 mm (mean=601, SD=145.8, n=166; Fig. 1). The sex ratio of our sample was 1:1.1 (male:female) and was not significantly different from 1:1 (χ^2 test, P>0.05). Neither the slopes (P=0.464) nor the elevations (P=0.063) of the length-weight equations for male and female permit were significantly different. The pooled length-weight equation for sexed and unsexed fish was

$$\log_{10} WT = 2.803 \log_{10} FL - 4.078, \quad (n=488, r^2=0.996)$$

where WT = weight in grams; and
FL = fork length in mm.

Age and growth

When viewed with transmitted light, permit otoliths have opaque (dark) annuli that alternate with translucent (light) zones (Fig. 2). Proceeding from the otolith's core towards the otolith's proximal margin, annuli are regularly spaced along the sulcal ridge. In some individuals, the annuli are indistinct and irregular in appearance, which made age estimation difficult. We considered 51 otoliths (17.3%) from permit ranging in length from 243 to 916 mm to be unreadable. The length-frequency distribution of fish whose otoliths were considered unreadable was not significantly different from that of fish whose otoliths were considered readable (Kolmogorov-Smirnov two-sample test, D=0.144, P=0.32); thus, no particular length

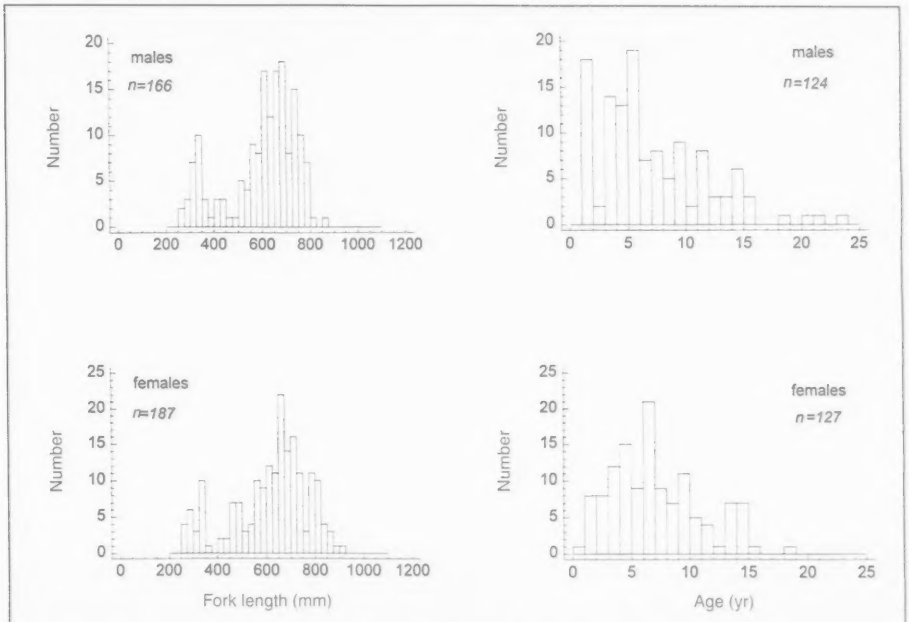

Figure 1

Fork lengths (mm) and ages (years) of male and female permit, *Trachinotus falcatus*, sampled from South Florida waters.

group of fish was systematically excluded from the age-and-growth analysis.

Annulus formation in permit occurs during spring and early summer. The percentage of permit with an annulus on the otolith's margin was greatest during summer and least during October–March, suggesting that annulus formation is seasonal and that annuli first become visible during late spring or early summer (Fig. 3). A single OTC-injected permit was successfully held for a sufficient length of time to be useful in age validation. This fish was captured and injected with OTC on 17 June 1993. The fish was sacrificed on 30 January 1996 and measured 600 mm in length. After 31 months in captivity, which included two spring-summer periods, the fish had formed two annuli, a number that is consistent with our hypothesis that a single annual mark forms annually during late spring or early summer. Also visible immediately before the OTC mark was an annulus that was probably formed during late spring of 1993, just prior to capture and OTC injection. Moreover, there was a wide margin subsequent to the last annulus that is consistent with the six or more months of otolith growth after formation of the final annulus in late spring or early summer of 1995.

Estimated ages of 298 permit ranged from 0 to 23 years for fish 102 to 900 mm long. Permit grew rapidly until about age five, and then growth slowed considerably (Table 1, Fig. 4). Most of the fish in our sample were less than 10 years old, although fish 10–15 years old were common. The oldest permit examined was a 23-year-old (781-mm) male (Table 1). Estimates of von Bertalanffy growth model parameters are presented in Table 2. The growth models for male and female permit were not significantly different (approximate randomization test, P=0.059).

Sexual maturation

We estimated that 50% of the males in the population reached sexual maturity by 486 mm and an age of 2.3 years, and 50% of the females in the population reached sexual maturity by 547 mm and an age of 3.1 years (Table 3). The smallest sexually mature male in our sample was 449 mm long, and the youngest sexually mature male was 3 years old. Our estimate of the age at 50% maturity for males was less than the age of the youngest mature male observed. This knife-edge maturity curve could be an artifact of our small sample size. The smallest sexually mature female in our sample was 476 mm long, and the youngest sexually mature female was 3 years old. All of the ovaries we examined contained primary-growth-stage oocytes. Cortical alveolar-stage oocytes occurred only in ovaries from permit larger than 450 mm and older than 2 years and were common only among permit larger than 500 mm and older than 3 years. Vitellogenic oocytes were found only in ovaries from fish larger than 550 mm and older than 3 years and were common only among permit larger than 600 mm. The length and age at which vitellogenic oocytes were commonly found agrees well with our estimate of the length and age at which 50% maturity was

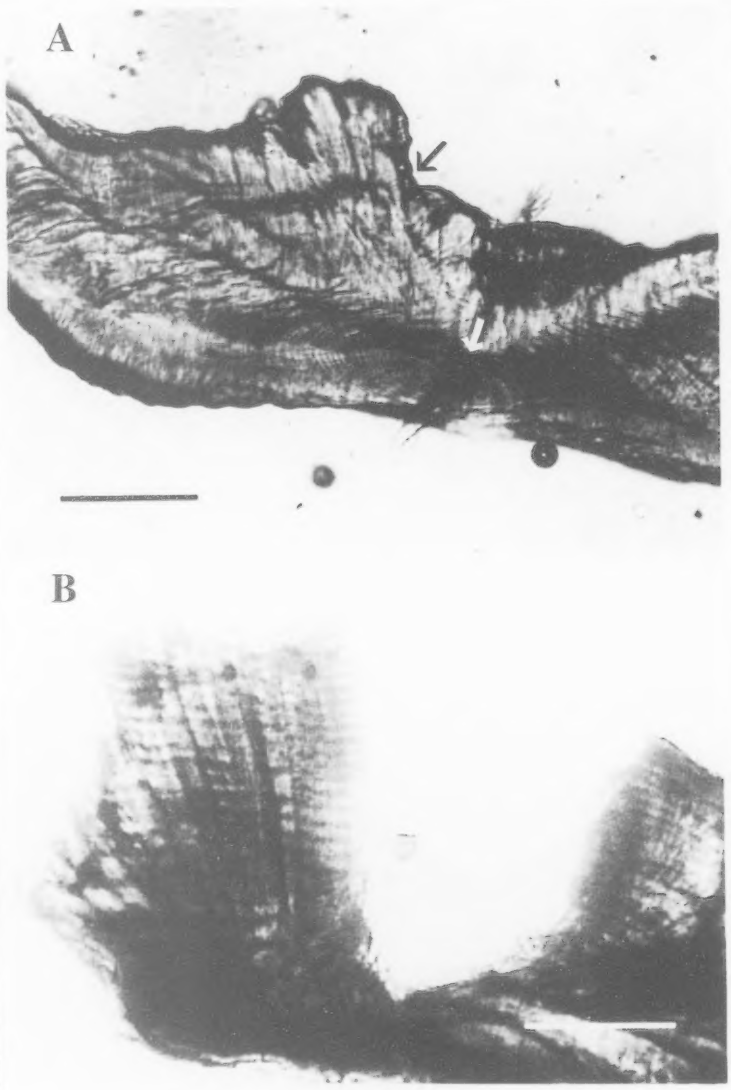

Figure 2

(**A**) Sectioned sagitta from a 1-year-old (363-mm-FL) permit, *Trachinotus falcatus*, collected in the Florida Keys on 27 February 1995, showing the location of the core (white arrow) and the first annulus (black arrow). Scale bar = 200 microns. (**B**) Sectioned sagitta from a 23-year-old male permit (781-mm-FL) collected in the Florida Keys on 4 June 1996. Scale bar = 500 m.

reached, suggesting that we misclassified few gonads with regression.

Spawning seasonality

Permit spawning appeared to be seasonal in the areas we sampled and occurred at least during May–July. We examined 15 permit ovaries that contained either oocytes in the final stages of maturation or POFs, structures indicative of imminent or recent (<24 h) spawning. We usually did not know the time of day when fish were caught, but all fish were captured during daylight hours (0700–1700 h). Oocytes in the final stages of maturation were found during June and July, and POFs were found

Table 1

Average observed and predicted fork lengths (mm) of permit, *Trachinotus falcatus*. The average observed length at age includes some seasonal growth that occurred after the formation of the final annulus. Values in parentheses are standard error and sample size.

	Sexes combined		Females		Males	
Age (yr)	Average observed	Predicted	Average observed	Predicted	Average observed	Predicted
0	160 (12.7;17)	139	277 (1)	212		149
1	301 (5.9;56)	319	310 (14.5;8)	353	334 (12.5;17)	337
2	476 (7.6;10)	447	479 (6.8; 8)	458	465 (33.5:2)	464
3	564 (10.1;27)	537	555 (12.1;13)	538	572 (15.9;14)	550
4	612 (6.3;28)	601	620 (9.8;14)	599	604 (7.6;14)	608
5	643 (8.7;29)	645	664 (13.8;10)	644	632 (10.5;19)	647
6	663 (8.7;26)	677	658 (10.7;20)	679	680 (9.3;6)	673
7	687 (12.0;17)	699	687 (10.8;9)	704	687 (23.6;8)	691
8	703 (16.9;12)	715	695 (22.7;7)	724	715 (27.4;5)	703
9	713 (15.1;21)	726	710 (26.8,11)	743	717 (13.3;10)	711
10	743 (30.0;6)	734	754 (34.2;5)	750	688 (1)	717
11	746 (21.8;12)	740	811 (25.3;4)	758	714 (23.2;8)	721
12	738 (35.3;5)	744	797 (0.5;2)	765	698 (46.9;3)	723
13	787 (19.4;9)	746	803 (26.2;6)	769	754 (15.7;3)	725
14	762 (19.5;13)	748	783 (12.8;7)	773	737 (38.9;6)	726
15	753 (13.4;4)	750	737 (1)	776	759 (17.3;3)	727
16		751		778		727
17		751		779		727
18	745 (48.5:2)	752	793 (1)	781	696 (1)	728
19		752		781		728
20	667 (1)	753	782		667 (1)	728
21	687 (1)	753	916 (1)	783	687 (1)	728
22		753		783		728
23	781 (1)	753	783		781 (1)	728

Table 2

Parameter estimates of the von Bertalanffy growth model for permit, *Trachinotus falcatus*, from South Florida waters. Values in parentheses are standard errors. FL = fork length.

Sex	n	L (mm FL)	K	t_0	adjusted r^2
Females	127	784.2 (13.79)	0.28 (0.027)	–1.12 (0.249)	0.833
Males	123	728.2 (9.52)	0.39 (0.034)	–0.58 (0.168)	0.855
Combined	297	753.1 (7.12)	0.35 (0.015)	–0.59 (0.065)	0.921

during May–July (Fig 5). Vitellogenic oocytes were most plentiful during March–July and were absent during October–December. No samples were available for histological examination in January or February, but it seems

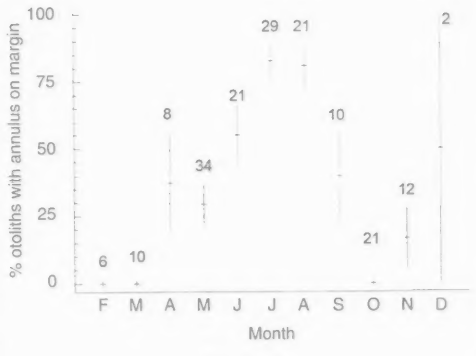

Figure 3

Mean percentage and standard error of permit (*Trachinotus falcatus*) otoliths with an annulus on the margin plotted by month. Numbers above the lines are the monthly sample sizes.

unlikely that spawning occurred during these months. Females with the greatest GSIs (>4%) were captured during March–August, and GSIs were least (<1.5%) during October–December (Fig. 6). Male GSIs were generally similar in magnitude to female GSIs and followed the same pattern.

In the Tampa Bay area, small permit (<40 mm) were present from June to November, suggesting that spawning extends into the fall. In the Florida Keys, small fish (<40 mm) were present all year, suggesting an extended spawning season, recruitment from other areas with different seasonal spawning patterns, or variable juvenile growth rates.

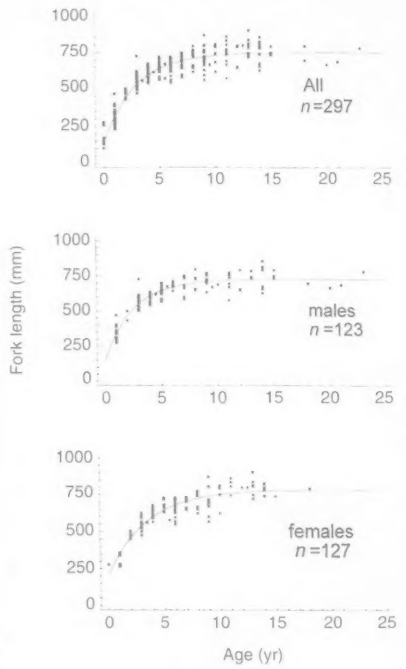

Figure 4

Observed and predicted fork lengths (mm) from the von Bertalanffy growth model for sexed and unsexed permit, *Trachinotus falcatus*.

Discussion

We obtained permit from a variety of fishery-dependent and fishery-independent sources; consequently, our sample is biased towards certain size classes, and the bimodal size-frequency distribution of our sample probably does not reflect that of the population or the Florida harvest. All the small fish (<300 mm) we examined were from fishery-independent sources; most large fish were from fishery-depen-

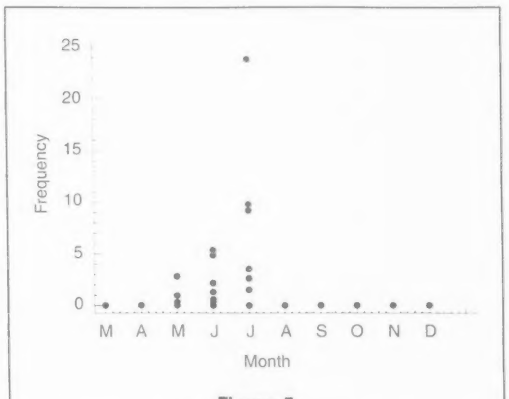

Figure 5

The percent frequency of occurrence of oocytes in the final stages of oocyte maturation (FOM) and postovulatory follicles (POF) in individual permit (*Trachinotus falcatus*) ovaries plotted by month.

Table 3

The relationship of percentage mature and fork length (mm) and the relationship of percentage mature and age (years) for permit, *Trachinotus falcatus*, from South Florida waters. *FL* = fork length (mm) and *AGE* = age (years). P_{50} is the absolute value of $((a+b)/c)$, is the inflection point of the curve, and is the length or age predicted by the logistic regression at which 50% of the permit in our sample were sexually mature. Sex is a dummy variable equal to 1 for males and 0 for females. PD is the adjusted percentage of deviance explained by the model.

		Percent female = $e^{(a+b(sex)+cX)}/(1+e^{(a+b(sex)+cX)})$				
X	*n*	*a*	*b*	*c*	PD	P_{50}
FL	314	–30.41 (6.336)	3.34 (1.087)	0.056 (0.0114)	0.84	486 mm (males) 547 mm (females)
AGE	233	–6.71 (0.878)	1.71 (0.576)	2.14 (0.238)	0.09	2.3 years (males) 3.1 years (females)

dent sources, such as charterboats. We did not sample any permit from the commercial fishery, which principally targets smaller fish as a result of the maximum size limit of 20 inches (508 mm FL) for permit caught by commercial vessels. Armstrong et al.[2] reported that most harvested permit in Florida were <440 mm. In contrast, our sample contained many fish larger than 600 mm. The high proportion of large permit in our sample could reflect a tendency for charterboats in the Florida Keys to select larger permit than those selected by more typical anglers statewide. Armstrong et al.'s[2] assessment was based on more systematic and statewide sampling than ours, and the differences between their sample and ours probably reflects our attempt to obtain a sample of all available size classes rather than a representative sample of the Florida harvest.

Age and growth

The oldest permit in our sample was estimated to be 23 years old. Although we examined many relatively large permit, larger fish than those we examined have been caught. Robins (1992) reported that permit can reach 1100 mm FL and a weight of 23 kg; consequently, permit longevity probably exceeds our estimate of 23 years. There are no other estimates of age and growth of permit for comparison, but our longevity estimates are similar to those determined from sectioned otoliths for other carangids. Manooch and Potts (1997) aged greater amberjack and found fish as old as 17 years. The oldest carangid yet studied is the trevally, *Caranx georgianus*, reported to reach an age of 46 years (James, 1984). The much smaller Florida pompano has been reported to reach an age of 7 years (Hood et al.[3]).

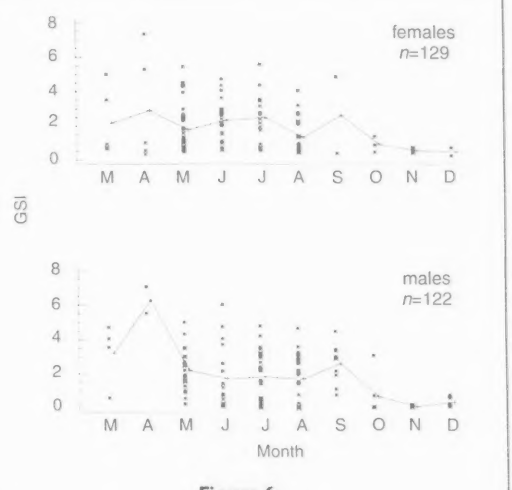

Figure 6

Gonadosomatic indices (GSI, •) and means (+) for sexually mature female and male permit, *Trachinotus falcatus*, plotted by month.

Our estimates of the von Bertalanffy growth model parameters are within the range of those reported for other carangids (James, 1984; Sudekum et al., 1991; Manooch and Potts, 1997). We found no significant differences between male and female von Bertalanffy growth models, but the significance level (P=0.059) was close enough to 0.05 to cause us to suspect that a difference might exist. Hood et al.[3] also found no sex-specific differences in growth models for pompano.

Sexual maturation

We sampled relatively few permit between 300 and 500 mm long, the size at which sexual maturity is reached. The lack of fish in this critical size range resulted in the knife-edge maturity curves. Larger sample sizes are needed to derive more precise estimates of age and size at sexual maturity. In an assessment of the status of permit stocks in Florida, Armstrong et al.[2] assumed that permit mature at about 440 mm FL on the basis of limited biological data available at the time. Our estimates of length at 50% maturity are larger: 486 mm for males and 547 mm for females. As a consequence of Florida's 20-inch (508-mm) recreational and commercial maximum size limit, most of the permit harvested are sexually immature (Armstrong et al.[2]).

Spawning

We believe that permit spawn over artificial and natural reefs in the waters of the middle and lower Florida Keys because ovaries of fish caught over these structures contained oocytes in the final stages of maturation and POFs. Other researchers have inferred that permit spawn in nearshore waters from the capture of early-stage larvae (Fields, 1962; Finucane, 1969). Permit ovaries that contained fresh POFs and oocytes in the final stages of maturation also contained clutches of early- and mid-stage vitellogenic oocytes, suggesting that permit are multiple-batch spawners.

Spawning occurred at least during May–June in the Florida Keys during 1995–97. Juvenile length frequencies in the Keys suggest a more prolonged spawning season—perhaps even year-round spawning; however, the prolonged presence of small juveniles could also be attributed to variable juvenile growth rates rather than extended spawning. This question could be resolved by direct aging of juveniles to evaluate growth rates. Our sample of adult permit may have been too small to reveal low levels of spawning outside of spring and early summer, and no mature permit were collected during January or February. On the basis of seasonal occurrence of juveniles, Finucane (1969) suggested that permit spawn during April–June in the Tampa Bay area, but Fields (1962) found juveniles

[3] Hood, P. B., D. T. Merryman, and D. J. Harshany. 1999. Age, growth, mortality, and reproduction of the Florida pompano, *Trachinotus carolinus*, from Florida waters. Unpubl. manuscript. Florida Marine Research Institute, 100 Eighth Avenue SE, St. Petersburg, FL.

year round suggesting a prolonged spawning period. Other carangids spawn during spring and summer: *Caranx ignobilis* and *Caranx melampygus* spawn during May–August in Hawaii (Sudekum et al., 1991) and *T. carolinus* spawns during January–August in Florida (Hood et al.[3]).

Our data suggest that maturation occurs at greater lengths than assumed by Armstrong et al.[2]; however, even using our maturation data, their observation that most permit landed are sexually immature remains true. With the current selectivity of the fishery, permit spawning stock biomass could decrease quickly in response to moderate levels of fishing mortality; thus, the regulations in place in Florida to restrict harvest levels appear to be justified. Significantly better estimates of the magnitude and age structure of the catch would be required to complete a comprehensive age-structured stock assessment.

Acknowledgments

We thank Capt. J. C. Wells, who provided us with most of the permit examined in this study and whose efforts made this work possible, and Don DeMaria, who also provided specimens. We thank John Swanson, Bill Gibbs, and the staff at the Keys Marine Laboratory for their assistance; Jim Colvocoresses, John Hunt, and others at the South Florida Regional Laboratory for their cooperation; and David Harshany, Heather Patterson, Dan Merryman, Graham Gerdeman, and Connie Stevens for their assistance. We also thank Jim Colvocoresses, Rich McBride, Jim Quinn, Judy Leiby, and Llyn French for helpful comments on the manuscript. This work was supported in part under funding from the Department of the Interior, U.S. Fish and Wildlife Service, Federal Aid for Sportfish Restoration F-59.

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Tag-reporting levels for red drum (*Sciaenops ocellatus*) caught by anglers in South Carolina and Georgia estuaries*

Michael R. Denson
Wallace E. Jenkins
Marine Resources Research Institute
South Carolina Department of Natural Resources
217 Ft. Johnson Rd.
Charleston, South Carolina 29422-2559
E-mail address (for W. E. Jenkins, contact author): jenkinsw@mrd.dnr.state.sc.us

Arnold G. Woodward
Coastal Resources Division
Georgia Department of Natural Resources
1 Conservation Way
Brunswick, Georgia 31523

Theodore I. J. Smith
Marine Resources Research Institute
South Carolina Department of Natural Resources
P.O. Box 12559
217 Ft. Johnson Rd.
Charleston, South Carolina 29422-2559

Abstract–A total of 1784 legal-size (≥356 mm TL) hatchery-produced red drum (*Sciaenops ocellatus*) were tagged and released to estimate tag-reporting levels of recreational anglers in South Carolina (SC) and Georgia (GA). Twelve groups of legal-size fish (~150 fish/group) were released. Half of the fish of each group were tagged with an external tag with the message "reward" and the other half of the fish were implanted with tags with the message "$100 reward." These fish were released into two estuaries in each state (n=4); three replicate groups were released at different sites within each estuary (n=12). From results obtained in previous tag return experiments conducted by wildlife and fisheries biologists, it was hypothesized that reporting would be maximized at a reward level of $100/tag. Reporting level for the "reward" tags was estimated by dividing the number of "reward" tags returned by the number of "$100 reward" tags returned. The cumulative return level for both tag messages was 22.7 (±1.9)% in SC and 25.8 (±4.1)% in GA. These return levels were typical of those recorded by other red drum tagging programs in the region. Return data were partitioned according to verbal survey information obtained from anglers who reported tagged fish. Based on this partitioned data set, 14.3 (±2.1)% of "reward" tags were returned in SC, and 25.5 (±2.3)% of "$100 reward" tags were returned. This finding indicates that only 56.7% of the fish captured with "reward" tags were reported in SC. The pattern was similar for GA where 19.1 (±10.6)% of "reward" message tags were returned as compared with 30.1 (±15.6)% for "$100 reward" message tags. This difference yielded a reporting level of 63% for "reward" tags in GA. Currently, 50% is used as the estimate for the angler reporting level in population models for red drum and a number of other coastal finfish species in the South Atlantic region of the United States. Based on results of our study, the commonly used reporting estimate may result in an overestimate of angler exploitation for red drum.

Manuscript accepted 1 August 2001.
Fish. Bull. 100:35–41 (2002).

There are major marine recreational fisheries along the south Atlantic and Gulf of Mexico coasts of the United States that target red drum, *Sciaenops ocellatus* (Matlock, 1986a; 1986b). During the late 1980s, overexploitation of red drum in many states resulted in the closure of commercial fisheries in most states and in the imposition of creel and size limits on catch of recreational anglers (McGurrin[1]) Concurrently, studies were initiated in a number of coastal states to gain a better understanding of red drum life history and to attempt to estimate exploitation rates. These investigations relied heavily on the use of fishery-dependent, mark-recapture studies to obtain the data necessary for creating a robust population model (McGurrin[1]).

Generic population models have been developed by using mark-recapture studies to estimate expected number of animals that survive and are recaptured from a year class within a given year (Brownie et al., 1985). Pollock et al. (1991) emphasized the need to modify tag recovery models in which data from multiyear tagging studies were used and suggested incorporating variables for postmarking survival and for reporting to estimate the recapture component of the model more accurately. The current model used to estimate recovery (recapture) rates of tagged fish (θ) includes a number of variables in an attempt to accurately account for what happens in nature ($\theta=\phi\mu\lambda$), where ϕ = tag retention multiplied by fish survival after tagging; μ = exploitation rate; and λ = reporting level (Hoenig et al., 1998). Reporting level (λ) of tagged fish captured by anglers is perhaps the most difficult variable to estimate accurately and is often assumed to be constant over time and geographic area (Hoenig et al., 1998).

* Contribution 467 of the South Carolina Department of Natural Resources, Charleston, South Carolina 29422-2559.

[1] McGurrin J. 1991. Fisheries management report 19 of the Atlantic States Marine Fisheries Commission. Fishery management plan for red drum—amendment 1, 123 p. Atlantic States Marine Fisheries Commission, 1400 16th St. NW Suite 310, Washington, D.C. 20036.

If the level of reporting can be closely estimated, then this estimated value can be incorporated into models that more accurately estimate survival and escapement (Hoenig et al., 1998).

In the past, researchers have attempted to accurately estimate reporting for marked animals in a number of ways. Some resource agencies have had creel clerks secretly implant tags into recreational anglers' creel during interviews, and others have conducted formal reward studies. For example, in Texas (TX), recreational anglers reported only 28% of a number of species of estuarine and marine finfish surreptitiously tagged by creel clerks (Matlock, 1981). A small-scale study during which red drum were surreptitiously tagged in Georgia (GA) also revealed low reporting levels (55%)(Woodward[2]). The GA study also noted trends in reporting by county and income level; however, because the number of tagged fish and subsequent returns in this study were small, valid statistical comparisons could not be made (Woodward[2]). Rawstron (1971) in a similar, more robust investigation conducted in freshwater lakes, found reporting levels of 50% for tagged bluegill, largemouth bass, and catfish and concluded that reporting appeared to be site and species specific.

Cash reward values ≤$50 have been used by many tagging programs to assess reporting levels (Rawstron, 1971; Matlock, 1981; Murphy and Taylor, 1991). In most cases, results have suggested that small cash awards do not provide adequate incentive for anglers to report capture of a tagged fish (Rawstron, 1971; Matlock, 1981; Murphy and Taylor, 1991). Work in California with stocked trout showed significantly higher reporting when a reward was offered, rather than no reward (Butler, 1962). Butler concluded that variability in reporting was also related to a number of other factors, including degree of publicity, angler interest in the fishery, and effort made to recover tags. Difficulty in determining reporting is not unique to fisheries population modeling. Historically, bands have been used to monitor populations of waterfowl and other birds. Reporting of banded waterfowl has also been shown to differ between locations (Henny and Burnham, 1976; Conroy and Blandin, 1984). For example, in areas where merchandise was regularly offered for banded birds, reporting decreased as compared with areas where capture of a marked bird was simply a novelty (Conroy and Blandin, 1984). Reward studies have attempted to overcome these problems by offering higher monetary rewards. In a study with waterfowl where rewards ranged from $5 to $1000, Nichols et al. (1991) demonstrated that there was a correlation between reporting and reward value. They also determined the asymptote for 100% reporting by duck hunters occurred between a reward value of $75 and $100. In a study of red drum in South Carolina (SC), Jenkins et al. (2000) found that $50 was not a high enough value to result in reporting differences between the standard "reward" message and a "$50 reward" message.

[2] Woodward, A. G. 1992. Evaluation of fish tag reporting by marine boat anglers in Georgia, 12 p. Georgia Department of Natural Resources, Coastal Resources Division, 1 Conservation Way, Brunswick, GA 31523.

For modeling purposes fishery managers in the south Atlantic region of the United States use reporting estimates of ~50% when analyzing return data for red drum. This approximate figure is used even though previous studies have shown that a number of variables may affect the accuracy of reporting tagged animals (Butler, 1962; Rawstron, 1971; Nichols et al., 1991; Ross et al., 1995; Woodward[2]). Assigning an approximate reporting level for the entire region could introduce bias in estimates of exploitation and potentially lead to significant exploitation of the population being managed. In previous studies where reporting levels for red drum and other finfish species were examined, there were a limited number of experimental units, making robust statistical analyses of the data difficult (Murphy and Taylor, 1991; Woodward[2]). This shortcoming is primarily due to logistical problems associated with capture, tagging, and release of sufficient numbers of similar-size wild fish in a manner that will ensure equal vulnerability to anglers over a large area (Yeager and Van Den Avyle, 1979; Murphy and Taylor, 1991). Our study attempts to reduce these problems by using similar-size hatchery-produced fish to carry tags. This experimental model allows a high degree of control over the design and implementation of a study (Jenkins et al., 2000). Further, fish can be tagged and stocked during seasons of the year when angler pressure is high, thereby minimizing the time required for data acquisition, as well as reducing variability associated with seasonal fluctuations in fishing effort (Jenkins et al., 2000). To assess the veracity of the currently used reporting estimate, a study was conducted in two estuaries in SC and two in GA. It was expected that the information obtained would provide a more accurate estimate for use in modeling red drum population dynamics in the south Atlantic region.

Materials and methods

All fish used in our study were progeny of locally captured wild broodstock. Adults had been spawned in tanks by using photoperiod and thermal conditioning (Roberts et al., 1978) at the SC Department of Natural Resources (SCDNR), Marine Resources Research Institute (MRRI) in Charleston, SC. Three day-old larvae were stocked in ponds at the SCDNR's Waddell Mariculture Center (WMC) in Bluffton, SC. When fish had grown to a mean total length (TL) of 200 mm, they were harvested and transported to MRRI. At MRRI, fish were grown to legal size (356 mm TL) in 4-m diameter tanks.

When fish were legal size (or approximately legal size), they were anesthetized in groups in a 0.1-g/L solution of MS-222 and culture water. Fish were then individually measured to the nearest mm and tagged with abdominal anchor tags (Floy Tag and MFG Co., Inc., Seattle, WA). In an effort to obtain results consistent with those from ongoing mark recapture programs in each state, fishery biologists from SC and GA tagged the fish to be stocked in their respective state. In addition, the tags used were identical to those used in ongoing studies in each state. For SC releases Floy model FM-95W tags were used.

These tags were completely orange and consisted of two parts: a 6.4-mm × 25.4-mm laminated disk wired to a 75-mm laminated streamer. The streamer portion contained the words "tag inside," a tag number, name of agency, and the reward message ("reward" or "$100 reward"). The disk portion contained the return address, reward message, a unique tag number, and the following: "reward, send tag, date, location, gear, length, phone number to …". Tags used in GA tags were also Floy tags (model FM-89SL). As in SC, the tag consisted of two parts. The laminated disk was slightly smaller (6.4 mm × 19 mm) and yellow, whereas the streamer was the same length (75 mm) and was the same color (orange) used for fish released in SC. The streamer did not contain the words "tag inside" but it did contain the rest of the information found on the SC streamers plus "return to…". The disk portion contained much of the same information found on the SC disk except "reward, send tag, date, location, gear, length, phone number to …". One half of the tags deployed in each state contained the message "$100 reward"; the remainder contained the message "reward." The "reward" message is the standard message that has been used for over 10 years in red drum mark-recapture studies in each state. Because of limitations in project funding and duration, the "$100 reward" tags also had an expiration date; "reward" tags, however, did not have an expiration date.

Figure 1

Map of coastal South Carolina (SC), Georgia (GA), and north Florida (FL) showing the location of each estuary where tagged red drum were released during the reward study.

After having been tagged, fish were retained in culture tanks for a minimum of one week to recover from handling. In preparation for release, marked fish were removed from the tanks and transported in oxygenated water, at a biomass density of ≤50 g/L, to the preselected estuaries. The estuaries in each state were as follows: Charleston Harbor and Calibogue Sound in SC; St. Simons Sound and Wassaw Sound in GA (Fig. 1). Three replicate release sites within each estuary were stocked with tagged fish. Upon arrival at each estuary, fish were acclimated for 1 hour to ambient water conditions prior to being transferred to holding tanks in boats. Within each estuary, the selected stocking sites had similar habitat characteristics and were geographically separate (≥5 km). At each site, fish were released individually approximately every 20 meters along the edge of the salt marsh to minimize the possibility of schooling behavior and subsequent multiple captures by individual anglers.

A total of 1774 fish were tagged and released during the project. Approximately 150 fish were released at each stocking site within each estuary (Table 1). Equal numbers of fish released at each site contained "reward" or "$100 reward" tags. Fish were released into Charleston Harbor, SC, and St Simons Sound, GA, during the fall of 1996 and into Calibogue Sound, SC, and Wassaw Sound, GA, during late spring and early summer 1997 (Table 1, Fig. 1). The expiration date for "$100 reward" tags deployed in fall 1996 was 31 March 1997, and for spring and summer 1997 releases, the expiration date was 31 December 1997. Neither the study nor the releases were publicized in any way other than by the normal information provided by ongoing tagging programs in each state. Captured tagged fish were reported directly to the respective Department of Natural Resources in each state. Participants who returned tags inscribed with "reward" received a prize that would normally be awarded by each agency (e.g. T-shirt or hat) and those reporting a "$100 reward" tag received a state-issued check for that amount.

Our study was based on two assumptions: 1) $100 was an adequate incentive to maximize reporting (assumed ~100%) of captured tagged fish; 2) the quotient of returns (the number of "reward"-inscribed tags divided by the returns of "$100 reward" tags) would yield the angler reporting level (λ) for the standard "reward" tag. Tags were returned in either of two ways: phone message or mail. All anglers who reported tags were later interviewed. During the interviews respondents were asked to confirm their reporting information and to express their attitudes and

Table 1

Cumulative data on release locations and stocking dates for fish, and both number of tags released and returned for each reward message.

		Tag			
		"Reward"		"$100 reward"	
Release location	Stocking date	No. released	No. returned	No. released	No. returned
Charleston Harbor					
site 1	31 Oct 1996	75	16	75	21
site 2	31 Oct 1996	75	18	75	21
site 3	31 Oct 1996	75	18	75	16
St. Simons Sound					
site 1	13 Nov 1996	75	10	75	17
site 2	13 Nov 1996	74	11	74	11
site 3	13 Nov 1996	75	10	75	15
Wassaw Sound					
site 1	8 May 1997	73	31	73	42
site 2	8 May 1997	75	23	75	29
site 3	8 May 1997	68	10	68	18
Calibogue Sound					
site 1	5 Jun 1997	75	9	75	21
site 2	9 Jul 1997	73	19	73	23
site 3	10 Jul 1997	74	9	74	12

opinions about the reporting procedure. All participants were asked the same questions from a standardized survey script. During the interview no information was provided to the anglers about the study design.

For statistical analysis each release site was treated as a replicate. By nesting site within estuary, within state, differences associated with each site, estuary, and state could be treated in the analysis to assess influence of the reward messages. The study design was a 2×2 factorial design (state and reward) with three levels of nesting (state, estuary, and site) (Table 1). Owing to differences in growth rates, insufficient numbers of legal-size fish were available to stock all estuaries during the same month. Thus one estuary in each state was stocked in the fall of 1996 and the remaining estuaries were stocked the following spring and summer. However, each stocking group was available for capture during the fall season when fishing pressure is heaviest (Wenner[3]). Percent return data were arcsine square-root transformed prior to analysis. Return data were analyzed by using a two-way analysis of variance (ANOVA) with significance determined at $P \leq 0.05$. The initial analysis examined all reported or "cumulative" data. The data were then partitioned in two additional ways: by single returns and survey data.

Single returns

This data set was the most restrictive. The assumption was that the partitioned data would be free of any potential bias associated with captures of multiple fish, or with monetary rewards or interactions with project staff.

Survey data

The data were partitioned according to the angler's answers during the interview to determine whether the inducement of a $100 dollar reward changed his or her reporting behavior. This data set included all tags reported individually, all tags of the same message reported as multiples, and all $100 tags. However, it excluded "reward" tags in instances where answers during the interview suggested that the angler's behavior had been changed by capturing a fish with a "$100 reward" tag.

Mean data for each of these analyses were reported with standard errors.

Results

Nearly 95% of tags that were returned were reported within 160 days after release of fish. More fish with "reward" tags were reported than those with "$100 reward" tags in one of the 12 release sites. Overall in SC, 151 anglers reported capture of 203 fish with tags. Anglers reported capture of 1–9 red drum per trip. One hundred

[3] Wenner, C. 1997. Personal commun. South Carolina Department of Natural Resources, 217 Ft. Johnson Rd. Charleston, SC 29422-2559.

and nineteen anglers in SC (79.0% of total anglers) reported only one tagged fish during the study. In GA, 184 anglers reported capture of 226 tagged fish. Single reports in GA represented 80.4% (n=148) of the total catch of tagged fish. The overall return level for all fish reported in SC (22.7 [±1.8]%) was not significantly different from that in GA (25.8 [±4.1]%) (P=0.8129, F=0.07) (Table 2). For the cumulative data, no significant differences were detected between "$100 reward" (27.8 [±3.3]%) and "reward" tags (20.8 [±2.7]%) (P=0.0724, F=12.33) (Table 2). There were also no statistical differences in the cumulative data among the estuaries within states (P=0.0604, F=4.07) (Table 2) and no detectable interaction between state and reward or reward and estuary within states, from the high variability in the cumulative data among estuaries and sites (52.5% and 47.5% of total variation, respectively).

Single returns

To further restrict the potential for bias caused by interaction of different reward messages or caused by the project biologist, capture reports were partitioned to include instances where an angler returned only one tag during the entire study. Overall, no significant differences (P=0.1215, F=6.76) were detected between the single returns of "reward" (11.6 [±1.1]%) and "$100 reward" (15.0 [±2.5]%) treatments within SC. This was also the case in GA (P=0.1215, F=6.760 where 15.1(±2.9)% of "reward" tags were returned, as compared with 17.6 (±2.7)% for "$100 reward" tags (Table 3). In addition, when data were compared between states, no differences were detected (P=0.6152, F=0.35). However, when single returns among estuaries were compared, Wassaw Sound in GA (Fig. 1) yielded significantly higher returns (P=0.0126, F=7.95) than any of the other estuaries where fish were released (Table 3).

Survey data

In SC, 52% of respondents indicated that they had previously caught tagged fish. Of those, several anglers admitted that they had not routinely reported tags. Additionally, others (16%) indicated that they would not have reported the tag if it had not been worth $100. In one extreme case an angler who reported six "$100 reward" tags and an equal number of "reward" tags at once, indicated that he would not have turned in an individual "$100 reward" tag because in his words "he did not need the money."

In GA, 29% of anglers had caught a tagged fish prior to the study; however only 7 (5%) said that they would not turn in tags worth less than $100. In light of this information, the return data were partitioned to eliminate potential bias that would result from encountering a "$100 reward" tag. This partitioned data set revealed that significantly fewer (P=0.0310, F=30.81) unbiased "reward" tags (14.3 [±2.1]%) were returned in SC than "$100 reward" tags (25.5 [±2.3]%) (Table 4). This was also true in GA, where 19.1(±4.3)% of "reward" tags were unbiased returns, as compared with 30.1 (±6.4)% of "$100 reward" tags ($P$=0.0310, F=30.81) (Table 4).

Table 2

Cumulative mean return level (%) and standard error for red drum tagged with one of two reward messages ("reward" or "$100 reward"). No significant differences were detected between reward message, estuary, or state.

	Return level	
Release location	"Reward" (%)	"$100 reward" (%)
Charleston Harbor	23.1 ±0.9	25.8 ±2.2
Calibogue Sound	16.7 ±4.7	25.2 ±4.6
South Carolina (mean)	19.9 ±2.6	25.5 ±2.3
St. Simons Sound	13.9 ±0.6	19.2 ±2.2
Wassaw Sound	29.3 ±8.0	40.9 ±9.0
Georgia (mean)	21.6 ±5.0	30.1 ±6.4
Overall mean	20.8 ±2.7	27.8 ±3.3

Table 3

Mean tag return level (%) and standard error for red drum tagged with one of two reward messages ("reward" or "$100 reward"). There were no significant differences in return levels by reward message within or among estuaries with the exception of those from Wassaw Sound which were significantly higher (P<0.05 noted by *) for both reward messages than any other estuary. SC = South Carolina; GA = Georgia.

	Tag message	
Release location	"Reward" (%)	"$100 reward" (%)
Charleston Harbor, SC	13.3 ±1.6	15.1 ±5.3
Calibogue Sound, SC	9.9 ±1.0	14.8 ±2.0
South Carolina (mean)	11.6 ±1.1	15.0 ±2.9
St. Simons Sound, GA	9.9 ±1.6	13.0 ±1.6
Wassaw Sound, GA	20.2 ±3.8*	22.1 ±3.7*
Georgia (mean)	15.1 ±2.9	17.6 ±2.7
Overall mean	13.3 ±1.6	16.3 ±1.8

Discussion

Overall return levels for the tagged fish released in our study were similar to levels of angler return for red drum in each state's fishery-dependent tagging programs (Wenner[3], Woodward[4]). Because of high variability within estuaries, there were no significant differences between returns of "reward" and "$100 reward" according to the analysis of cumulative return data. The high variability

[4] Woodward, A. G. 1997. Personal commun. Georgia Department of Natural Resources, 1 Conservation Way, Brunswick, GA 31523.

Table 4

Mean return level (%), standard error, and range for unbiased data (adjustments based on verbal interviews) for red drum tagged with one of two reward messages ("reward" or "$100 reward"). Return data for the "$100 reward" message were significantly higher ($P<0.05$) for each estuary, state, and overall than those for the "reward" message.

	Tag message		Unbiased reporting level[1] (%)	
Release location	"Reward" (%)	"$100 reward" (%)	Mean	Range
Charleston Harbor	17.3 ±1.3	25.8 ±3.9	67.1	57–78
Calibogue Sound	11.3 ±6.3	25.2 ±8.0	44.8	19–67
South Carolina (mean)	14.3 ±5.2	25.5 ±5.6	56.7	—
St. Simons Sound	11.7 ±2.1	19.2 ±3.9	60.9	41–82
Wassaw Sound	26.5 ±10.4	40.9 ±15.7	64.8	56–79
Georgia (mean)	19.1 ±10.6	30.1 ±15.6	63.4	—
Overall mean	16.7 ±6.2	27.8 ±11.5	60.1	19–82

[1] Example: Charleston Harbor: "$100 reward" tags reported = 100%: 17.3/25.8 = 67.1% reporting level for "reward" tags.

between sites within the same estuary was unexpected. In addition, variation between estuaries in the same state made comparisons between states difficult. However, "reward" tags were returned less often than "$100 reward" tags from 11 of the release sites in the unpartioned data set. After identifying and excluding possible sources of bias, we found that there were statistically significant differences between reporting level of "reward" and "$100 reward" tags in all areas (Table 4). The range of 19–82% in levels of reporting between sites was more variable than anticipated (Table 4). Removal of the suspected biased anglers from the data set resulted in a mean unbiased reporting level of 67.1% in Charleston Harbor and 44.8% in Calibogue Sound (Table 4). Unbiased reporting in GA was somewhat higher than in SC (63.4% vs. 56.7%). The fact that significant differences were found only after biased angler data were removed from the data set illustrates that a small number of skilled anglers can have an effect on fisheries-dependent data. Their failure to report tags may be due to a lack of novelty in encountering tagged fish, or to insufficient reward incentives (having already received a number of t-shirts, fishing caps, etc.). These data suggest that use of noncash rewards is beneficial only for the first time an angler catches a tagged fish and decreases as anglers catch additional tagged fish. Further repeated exposure to tagging programs within each state eventually results in angler ambivalence and reduced cooperation. This indifference is of particular concern with the use of a constant regional reporting rate as described by Hoenig et al. (1998). A decreasing rate of tag return could be mistaken for lower harvest, reduced fishing effort, poor survival, or increased population size.

Lack of differences in reporting levels between "reward" and "$100 reward" in the single-return (one fish) partition of data (Table 3) confirms that anglers who capture many tagged fish per trip or per season (who were omitted from this data set) significantly influence reporting. Single return-data also suggest that anglers who catch fewer fish (tagged or not tagged) are more likely to report captures of tagged fish regardless of reward amount. Considering the impact a few skilled anglers can have on tag reporting estimates, these results demonstrate the need for further evaluation of the interaction between tagging programs and angler behavior. The 50% reporting level currently used by managers is approximately a 17% underestimate (50/60=0.83) of actual reporting recorded for the red drum fishery in SC and GA. Continuing to use the 50% reporting estimate for this fishery will be more conservative than using the actual reporting level (λ) to calculate angler recovery rate (θ). Reporting was also extremely site specific, and application of data from one site to a broader area may not be appropriate. Ideally tag-recapture models should be weighted by site-specific reporting information to account for this variability which could be accomplished by regular deployment of high value (≥$100) reward tags within each system to gauge angler reporting. Even if offering a $100 does not result in 100% reporting, as Nichols et al. (1991) suggested, it may yield the highest reporting possible with monetary incentives, meaning that our unbiased reporting may have been slightly overestimated. Regardless, this approach is still more accurate than that of adopting a regional average. Our results emphasize that researchers need to conduct controlled tag reward studies regularly and also to offer sufficient rewards in order to avoid under reporting. Furthermore, tag reports must be followed up with angler interviews to determine attitudes and give managers an opportunity to remove bias from the data (Reinecke et al., 1992, Zale and Bain, 1994, Pegg et al., 1996).

Acknowledgments

We would like to thank the staff of the Inshore Fisheries Sections of the SCDNR and GADNR for tagging, distribution of fish and tag collection and processing. We especially thank John Fortuna and Carolyn Belcher for their assistance with statistical design and data analysis. We

also thank Charlie Bridgham and Allan Hazel, for production, maintenance, and transportation of fish, and Charlie Wenner, for reviewing this manuscript and providing valuable insights during the project. The study was funded in part by USDOC, NMFS the Saltonstall-Kennedy Program grant #A67FD0031 and NA77FD0062 and the state of South Carolina.

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Age, growth, and mortality of the Mayan cichlid (*Cichlasoma urophthalmus*) from the southeastern Everglades

Craig H. Faunce
Estuarine and Marine Research Group
Tavernier Science Center, Audubon of Florida
115 Indian Mound Trail
Tavernier, Florida 33070
E-mail address: cfaunce@audubon.org

Heather M. Patterson
Florida Marine Research Institute
Florida Fish and Wildlife Conservation Commission
100 Eighth Avenue SE
St. Petersburg, Florida 33701-5095

Jerome J. Lorenz
Estuarine and Marine Research Group
Tavernier Science Center, Audubon of Florida
115 Indian Mound Trail
Tavernier, Florida 33070

Abstract–Mayan cichlids (*Cichlasoma urophthalmus*) were collected monthly from March 1996 to October 1997 with hook-and-line gear at Taylor River, Florida, an area within the Crocodile Sanctuary of Everglades National Park, where human activities such as fishing are prohibited. Fish were aged by examining thin-sectioned otoliths, and past size-at-age information was generated by using back-calculation techniques. Marginal increment analysis showed that opaque growth zones were annuli deposited between January and May. The size of age-1 fish was estimated to be 33–66 mm standard length (mean=45.5 mm) and was supported by monthly length-frequency data of young-of-year fish collected with drop traps over a seven-year period. Mayan cichlids up to seven years old were observed. Male cichlids grew slower but achieved a larger size than females. Growth was asymptotic and was modeled by the von Bertalanffy growth equation L_t=263.6(1–exp[–0.166(t–0.001)]) for males (r^2=0.82, n=581) and L_t=215.6 (1–exp[–0.197(t–0.058)]) for females (r^2= 0.77, n=639). Separate estimates of total annual mortality were relatively consistent (0.44–0.60) and indicated moderate mortality at higher age classes, even in the absence of fishing mortality. Our data indicated that Mayan cichlids grow slower and live longer in Florida than previously reported from native Mexican habitats. Because the growth of Mayan cichlids in Florida periodically slowed and thus produced visible annuli, it may be possible to age introduced populations of other subtropical and tropical cichlids in a similar way.

Manuscript accepted 1 August 2001.
Fish. Bull. 100:42–50 (2002).

The Mayan cichlid, *Cichlasoma urophthalmus* (Günther), is native to the fresh and brackish waters of the Atlantic slope of Central America from Mexico to Nicaragua (Miller, 1966), where it is exploited commercially in artesanal fisheries and aquaculture (Martinez-Palacios and Ross, 1992). The first collections of the Mayan cichlid in the United States were made in 1983 from a freshwater habitat and a mangrove creek within Everglades National Park, Florida (Loftus, 1987). Although it remains unknown how or where Mayan cichlids first entered Florida waters, there is evidence that the discovery of this exotic fish was made shortly after their introduction (Loftus, 1987). Since their discovery, Mayan cichlids have expanded their range to include a variety of habitats from Naples (26°05′N, 81°48′W) to West Palm Beach (26°45′N, 80°04′W). The species remains abundant in the man-made freshwater canals and estuarine mangrove habitats of the region (Trexler et al., 2000).

The introduction of the Mayan cichlid into southern Florida has had both economic and ecological significance. This species supports a small sport fishery because it is edible, attractive, and aggressively takes baits and artificial lures (Shafland, 1996). Anglers, however, have mixed feelings towards this fish because it readily takes artificial baits and fights hard on light tackle, and it can interfere with the pursuit of larger gamefishes, such as the common snook (*Centropomus undecimalis*). In some areas, the Mayan cichlid is the most common fish caught by recreational anglers and is targeted by subsistence anglers. There is concern, however that the interaction between Mayan cichlids and native fishes could alter the ecology of the Everglades and Florida Bay region. Although the role of Mayan cichlids as food for higher trophic-level fishes has not been quantified, they themselves are omnivorous and prey upon native fishes (Martinez-Palacios and Ross, 1988; Howard et al.[1]).

Previous studies of the Mayan cichlid have focused almost entirely on its suitability for aquaculture in Mexico (e.g.

[1] Howard, K. S., W. F. Loftus, and J. C. Trexler. 1995. Seasonal dynamics of fishes in artificial culvert pools in the C-111 basin, Dade County, Florida. Final Rep. CA5280-2-9024, 34 p. and append. South Florida Research Center, Everglades National Park, Homestead, FL.

Martinez-Palacios and Ross, 1986; Flores-Nava et al., 1989; Ross and Beveridge, 1995) and on the potential for range expansion in the United States (e.g. Stauffer and Boltz, 1994). Few studies have addressed the life history of the Mayan cichlid, and only scant information exists on the age structure and growth rate of this species. From the seasonal length-frequency distributions for Celestun Lagoon, Mexico, Martinez-Palacios and Ross (1992) concluded that Mayan cichlids from 70 to 130 mm standard length had completed their first spring and were reproductively active, whereas individuals from 131 to 200 mm standard length had entered their second reproductive year. Observing no fish >200 mm, Martinez-Palacios and Ross (1992) concluded that the population of Mayan cichlids in the lagoon comprised fast-growing fish with one, or two (rarely), reproductive seasons in their lifetimes. Aging of Mayan cichlids using a validated method is needed to determine the accuracy of previously reported age and growth estimates and to compare the age structure between populations from Mexico and Florida. Here we provide a first account of the age, growth, and mortality of the Mayan cichlid from Florida waters.

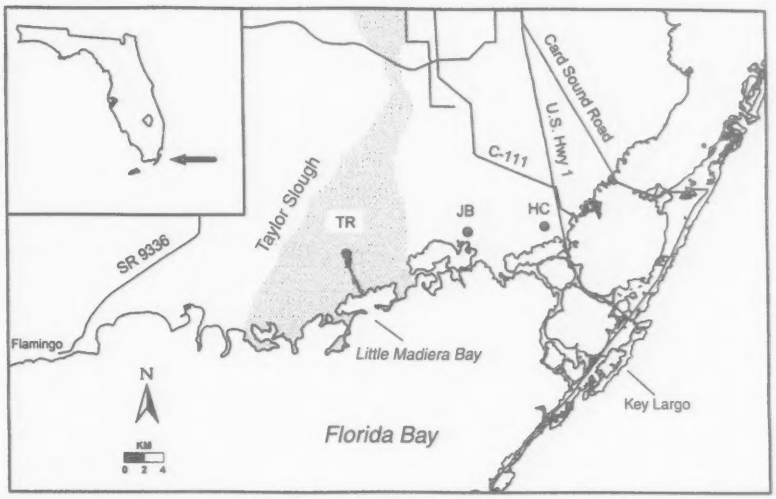

Figure 1

Map of southeastern Florida showing sampling locations (TR=Taylor River, JB=Joe Bay, HC=Highway Creek).

Methods

Mayan cichlids were collected from the dwarf mangrove forests of southeastern Florida. This habitat is dominated by small (0.5–2.0 m tall) red mangrove trees (*Rhizophora mangle*) in an expansive, seasonally inundated wetland of typically shallow water (average maximum depth=30 cm). These mangroves increase in canopy width and height nearer to continuously inundated deeper creeks. The system is inundated mostly by fresh water during July–February but becomes more saline (10–35‰) during the dry season (March–June).

Cichlids <65 mm standard length (SL) were collected by using drop traps (Lorenz et al., 1997) to determine when Mayan cichlids first recruit. Drop-trap samples were collected every six weeks from August 1990 to September 1996 at Highway Creek, Joe Bay, and Taylor River (Fig. 1). Larger cichlids (>65 mm SL) were collected by using hook-and-line gear comparable to that used in other studies (Martinez-Palacios and Ross, 1992). Hook-and-line collections were conducted monthly from March 1996 to October 1997 in Taylor River, a major freshwater distributary of the Everglades emptying into northeastern Florida Bay. Each fishing effort continued until approximately 40 fish were obtained. Fish collected by both methods were measured (SL and total length [TL], mm), weighed to the nearest 0.1 gram, and their sex was determined macroscopically when possible (Faunce and Lorenz, 2000). Fish captured during 1994–97 were used for age-and-growth analyses. All lengths reported hereafter are standard lengths.

Sagittal otoliths were removed, blotted dry, and stored in vials until they were sectioned. The left sagitta, unless broken, was used for age determination. Otoliths were sectioned by using a low-speed Beuhler Isomet saw with diamond blade. Three or four 0.5-mm thick transverse sections, one through the core, were cut and mounted on microscope slides with Histomount™ adhesive and allowed to dry. Sagittae from fish <100 mm were embedded in Spurr, a high-density plastic medium (Secor et al., 1992) and a 1–2 mm thick transverse section containing the otolith core was then cut. The sections were mounted on a microscope slide with Crystal Bond™ 509 adhesive, and polished with wet and dry sandpaper of grit sizes 220–2000 until growth rings were visible. A polishing cloth with 0.05-gamma alumina powder was used to remove scratches.

A standardized protocol for interpreting otolith growth zones was followed. When viewed with reflected light, the transverse sections of Mayan cichlid otoliths had two distinct regions: 1) an "inner region" extending from the core to the first visible opaque zone (ring), and 2) an "outer region" extending from the first visible opaque zone to the edge of the otolith (Fig. 2). The inner region was typically more opaque than the outer region and sometimes contained a visible growth zone or numerous check marks, or both. Unfortunately, these marks were difficult to interpret, inconsistent between sections from individual fish, and in many cases absent altogether. Consequently, we did not count any marks from the inner region in our age estimations. However, the translucent appearance of the outer region of the otolith made it possible to count distinct, separate, opaque rings when present. The number of rings

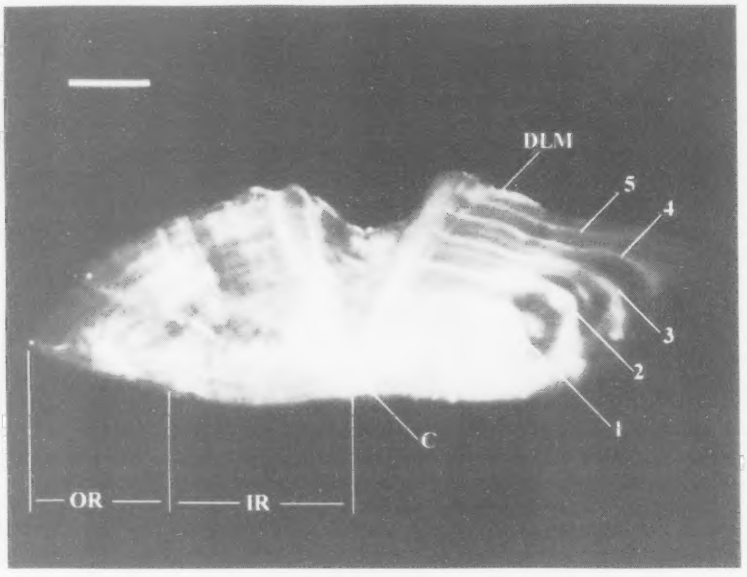

Figure 2

Transverse section of a six-year-old Mayan cichlid (*Cichlasoma urophthalmus*) otolith showing the outer region (OR), inner region (IR), and five visible annuli (1–5). Note that the first annulus (1) corresponds to the fish's second year of growth. A ring corresponding to the first year of growth was not consistently visible and was therefore not counted. Measurements for marginal-increment analysis were made on an axis adjacent to the sulcal ridge from the core (C) to the dorsolateral margin (DLM). Scale bar=500 μm.

on each otolith section was counted independently by two readers using compound microscopes, and the results were compared. If there was a discrepancy in the counts between readers, the section was re-examined. If a consensus could not be reached between the readers after the third reading, the otolith was excluded from the study.

Linear regression was used to determine the relationship of otolith radius to standard length and marginal-increment analysis was used to determine the periodicity of ring formation. Distance from the core to the proximal edge of each ring and to the dorsolateral margin of the otolith (otolith radius) was measured (Fig. 2). Measurements were made with a digital-image processing system along an axis adjacent to the sulcal ridge. The distance from the outermost ring to the dorso-lateral margin (i.e. marginal increment=MI) was plotted by month (marginal increment analysis). Because the majority of Mayan cichlids in Taylor River spawn during May and June (Faunce and Lorenz, 2000), and ring formation occurred during January–May, we assigned each fish a biologically realistic median hatching date of 1 June. Fish collected prior to 1 June that had not yet formed a new opaque ring (=high MI), and all fish collected after 1 June, were assigned a yearly age equal to their ring count. Fish collected before 1 June that had already formed a new opaque ring (i.e. an "early" ring) were assigned a yearly age of one less than their ring count. To compare the timing of ring formation between age groups, marginal-increment analysis was performed on pooled ages 0–3 and 4–7 because our monthly sample sizes for individual age classes were insufficient for this analysis.

We used linear regression to determine the relationship between standard length and total length for all hook-and-line caught fish. The relationship between standard length and total weight was calculated separately for each sex with $\log_{10}$-transformed data. Analysis of covariance (ANCOVA) was used to test for significant differences between the slopes and intercepts of male and female length-weight relationships. Length-frequency distributions for males and females caught with hook-and-line were compared by using the Mann-Whitney rank sum t-test. Nonlinear least squares procedures (SAS, 1989) were performed on final observed age-at-length data to estimate parameters for the von Bertalanffy growth equation

$$L_t = L_\infty\left(1-\exp[-K(t-t_0)]\right),$$

where L_t = the standard length (mm);
L_∞ = the asymptotic length;
K = the Brody growth coefficient;
t = the age (years); and
t_0 = the age at zero length (von Bertalanffy, 1957).

To increase the number of observations used for fitting the growth model, we back-calculated past size-at-age information for each sexed fish using the Fraser-Lee method following Devries and Frie (1996);

$$L_i = \left[(L_c - a)/S_c\right]S_i + a,$$

where L_i = the back-calculated length of fish when the i^{th} increment was formed;
L_c = the length of fish at capture;
S_c = the otolith radius at capture; and
S_i = the otolith radius at the i^{th} increment.

The slope, $(L_c - a)/S_c$, was calculated for each fish as the slope of a line connecting two points: (S_c, L_c) and $(0, a)$. The y-intercept parameter a was determined from the relationship between otolith radius and standard length for all fish, and should approximate the fish length at which otolith radius equals zero (Devries and Frie, 1996). Because we could not accurately determine the sex of each fish <70 mm, fish whose sex could not be determined were included in the fitting of both male and female growth curves.

Catch curves were analyzed with two methods to determine annual mortality rates for Mayan cichlids. Survival rate (S) and its respective variance were estimated by using the empirical abundance data (Robson and Chapman, 1961) and the regression of the natural logarithm of year-class abundance (Ricker, 1975). The instantaneous rate of mortality (Z) was derived from the relationship $Z = -\ln(e^S)$. Total annual mortality (A) was computed as $A = 1 - S$. The age at full recruitment to the hook-and-line gear based on our catch curve was determined to be four years.

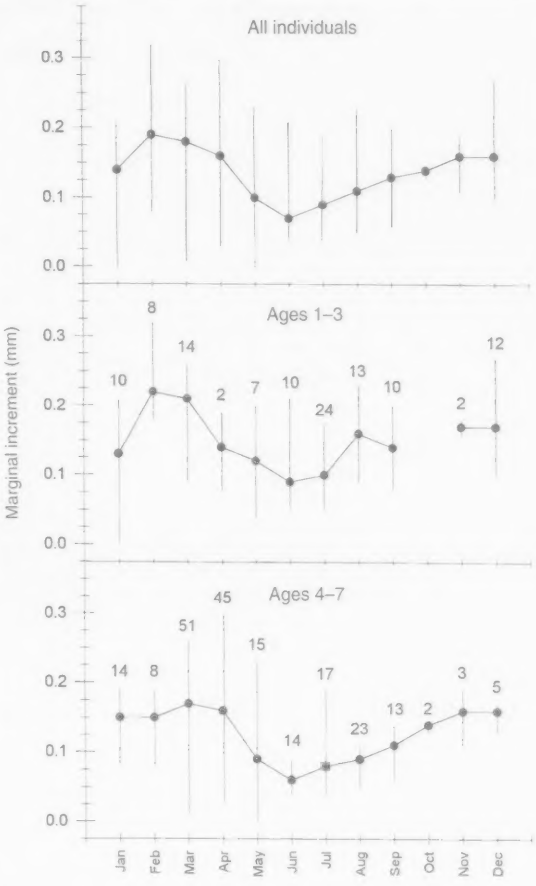

Figure 3

Monthly mean marginal increment and range for all Mayan cichlids and pooled age classes 1–3 and 4–7. Note the consistent annual minimum in June. Numbers indicate sample size.

Results

The fragile nature of Mayan cichlid otoliths caused a high proportion (54%) to be lost during the cutting process. However, only five of the 391 successfully sectioned otoliths were discarded because a consensus between readers could not be reached. A newly formed opaque ring was generally observed in fish captured January–May, and the mean monthly marginal increment reached a single yearly minimum in June for all age classes examined (Fig. 3). These data indicate that the opaque rings observed were annuli.

The growth of young-of-year Mayan cichlids collected with drop traps could be followed by the progression of modal length from monthly length frequencies. Newly recruited fish were present in August (mode=10 mm) and grew to a size of 50 mm by June (Fig. 4). An early spawning event in 1993 (senior author, unpubl. data) produced a smaller-size (20 mm) cohort that was observed in June. Fish with one annulus were much larger (50–149 mm, mean=97 mm) than the size of age-1 fish suggested from our drop-trap data (June mode=50 mm). This information, combined with the presence of marks in the inner region of the otolith, led us to conclude that the first annulus in our age estimations was laid down between January and May of the fish's second year of growth, and we added a year to each individual's total age.

Length-length and length-weight relationships are given in Table 1. As required by the Fraser-Lee method for back-calculation of size-at-age information, otolith radius and standard length were closely related ($SL = 131.2 \times OR + 4.0247$, $n = 371$, $r^2 = 0.80$). Analysis of covariance did not detect differences between the slopes of length-weight relationships for males and females ($F_{1,839} = 0.15$, $P = 0.696$) but did reveal significant differences between the respective intercepts for males and females ($F_{1,839} = 4.10$, $P = 0.043$).

The length of Mayan cichlids at a given age was modeled by the von Bertalanffy growth equation (Fig. 5). Predicted lengths fitted well with the final adjusted observed

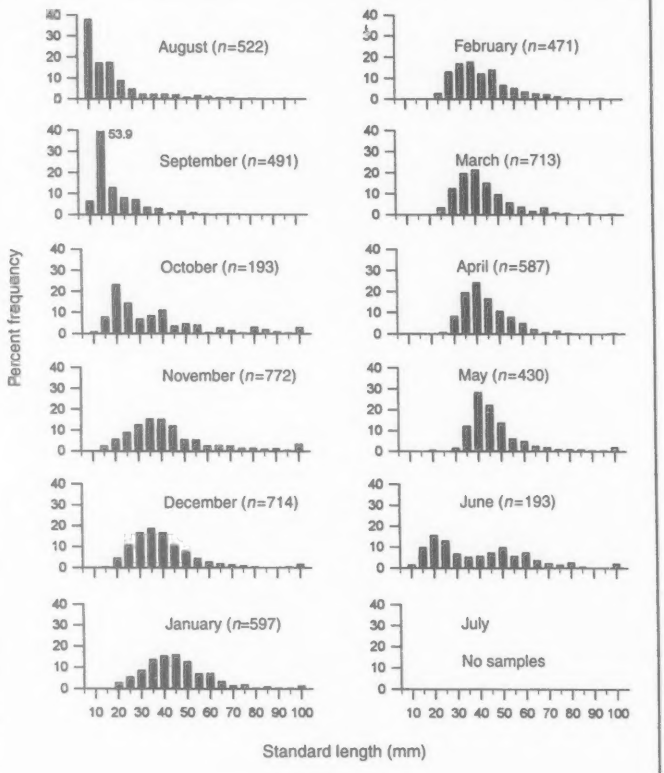

Figure 4

Pooled length-frequency histograms for Mayan cichlids collected with drop traps from 1990 to 1996.

and back-calculated length-at-age data for males (r^2=0.82, n=581) and females (r^2=0.77, n=639). Our observed and back-calculated size of age-1 fish (mean ±1 standard error=45.5 ±10.11 mm, range=33-68 mm, n=22) corresponded well with the modal length of age-1 fish collected in drop-trap samples (50 mm). Differences in the parameter estimates for the von Bertalanffy growth equation were observed for each sex. Males were larger than females for all ages (Table 2). Although males exhibited a slower growth rate (K) and larger maximum attainable size (L_∞) than females, the von Bertalanffy growth model parameters were not significantly different between sexes (95% CI, Table 3). Male and female Mayan cichlids up to seven years old were observed.

The size of fish examined ranged from 21 to 210 mm (median=127 mm, interquartile range=98 mm, n=1046). Males ranged from 69 to 210 mm (median=137 mm, interquartile range=119 mm, n=400), and females ranged from 58 to 190 mm (median=132 mm, interquartile range=115 mm, n=449) (Fig. 6). The length-frequency distribution for males was significantly larger than that for females (P<0.001). The overall ratio of males to females was 1:1.1.

Age-frequency distributions of Mayan cichlids collected by hook-and-line gear suggest that these fish are fully recruited to the fishery at age four (Fig. 7). The majority of males (85.1%) and females (81.5%) were 3–5 years old, and there was a significant difference (Mann-Whitney rank sum t-test, P<0.001) in the age-frequency distribution of males (median=3.67 years, interquartile range=2.12) and females (median=4.78 years, interquartile range=3.86). Total instantaneous mortality (Z), annual survival (S), and annual mortality (A), based on the regression of our catch-curve data, were estimated at 0.57, 0.56, and 0.44, respectively (r^2=0.91, n=3). Robson and Chapman (1961) estimates were Z=0.91, S=0.40 (±0.035), and A=0.60.

Discussion

Transverse otolith sections can be used to precisely age Mayan cichlids from Florida waters. There was a high congruence (98.7%) between the age estimations of each reader. Annuli corresponding to years 2–7 were clearly

Table 1

Length-length, length-weight, and otolith-radius–standard-length regressions for the Mayan cichlid, *Cichlasoma urophthalmus*, from Taylor Slough, Florida. Regressions are in the form $Y = a + bX$. *TL* = total length (mm); *SL* = standard length (mm); *WT* = total weight (g); *OR* = otolith radius (mm); range = sample standard length range in regressions. Values in parentheses are standard errors.

Y	*a*	*b*	*X*	*n*	Range (mm)	r^2
Sexes combined						
TL	0.6220 (0.2875)	1.3067 (0.0022)	*SL*	961	40–210	0.997
SL	–0.1281 (0.2202)	0.7631 (0.0013)	*TL*	961	40–210	0.997
SL	4.0247 (3.2740)	131.2092 (3.4214)	*OR*	371	33–210	0.800
$\log_{10}WT$	–4.2490 (0.0257)	2.9314 (0.0122)	$\log_{10}SL$	847	58–210	0.986
Males						
$\log_{10}WT$	–9.7958 (0.0874)	2.9329 (0.0178)	$\log_{10}SL$	395	84–210	0.986
Females						
$\log_{10}WT$	–9.7387 (0.0856)	2.9232 (0.0176)	$\log_{10}SL$	444	89–182	0.984

visible on the otoliths. The annulus corresponding to the first year's growth was not consistently clear to the readers, which has been observed in thin-sectioned otoliths of other fish species in Florida. Murphy and Taylor (1994) found that the first annulus was visible only in certain individuals of spotted seatrout, *Cynoscion nebulosus*. Similarly, Murphy and Taylor (1990) found that the annulus corresponding to the first winter or spring was absent in red drum, *Sciaenops ocellatus*. Direct validation of marked otoliths is needed to confirm the presence and location of the first annulus on the otolith of Mayan cichlids.

We observed differences in the growth patterns of males and females that are likely linked to reproduction. Males were larger than females and did not appreciably slow their growth with age. The nearly linear growth of males resulted in a theoretical maximum size (L_∞) of 263.6 mm, well above the ~200 mm commonly observed for this species (Loftus, 1987; Martinez-Palacios and Ross, 1992; present study). Larger males are common in riverine and lagoonal populations of tilapias (Cichlidae) and may have a selective advantage during the reproductive season if they can defend a spawning pit or brood against potential predators (Lowe-McConnell, 1982). Because sperm production requires less energy than egg production (Jalabort and Zohar, 1982), the slowed growth observed in females compared with that for males is likely due to differences in energy budgets during the reproductive season.

No significant differences were found by ANCOVA in the slopes of sex-specific length-weight relationships, but there were significant differences in the intercepts of those lines. Because the actual difference between the *y*-intercepts (weight) of each length-weight relationship was <0.001g, we attribute no biological meaning to the statistical difference and consider the length-weight relationships for both sexes to be equal.

Table 2

Average predicted and observed standard lengths (mm) for male and female Mayan cichlids.

Age (yr)	Predicted	Average observed	Standard error	*n*
Males				
1	40.3	45.5	2.2	22
2	74.4	74.3	1.12	148
3	103.4	102.0	1.24	152
4	127.9	127.1	1.36	139
5	148.7	147.8	1.66	88
6	166.3	173.0	2.56	28
7	181.1	206	1.32	4
Females				
1	36.4	45.5	2.16	22
2	68.4	70.6	1.05	156
3	94.7	96.8	1.31	160
4	116.3	119.8	1.4	151
5	134.0	137.0	1.59	102
6	148.6	148.1	1.94	45
7	160.6	151.0	3.22	3

Mayan cichlids in Florida were much smaller at a given age than those reported by Martinez-Palacios and Ross (1992) in Mexico. One-year-olds were 33–66 mm in Florida vs. 70–130 mm in Mexico, and age-2 fish were 44–130 mm

Table 3

Parameter estimates for the von Bertalanffy growth model (1957) for Mayan cichlids and associated standard error (SE) and confidence intervals (CI).

Sex	L_∞ (mm)	K	t_0 (yr)	n	r^2
Males	263.66	0.165	0.001	581	0.82
SE	25.15	0.027	0.124		
95% CI	49.28	0.053	0.243		
95% CI range	214.34–312.95	0.112–0.218	0.242–0.244		
Females	215.63	0.197	–0.058	639	0.77
SE	17.33	0.031	0.142		
95% CI	33.96	0.061	0.278		
95% CI range	181.67–249.59	0.136–0.258	–0.336–0.220		

in Florida and 131–200 mm in Mexico. We found a maximum age of seven years, whereas two years was suggested by Martinez-Palacios and Ross (1992). We offer three explanations for these observed differences in the length-at-age data. First, exploitation rates may differ between study areas. Fish in our study came from the Crocodile Sanctuary within Everglades National Park and had not been exposed to fishing mortality. Fishing for Mayan cichlids occurs outside of our study area, and heavy exploitation can select for faster-growing fish with a shorter lifespan (Ricker, 1975). Martinez-Palacios and Ross (1992) suggested that their population was overfished. Second, differences in temperature impact fish growth. Colder winter temperatures in Florida were sufficient to form seasonal marks in the otoliths of Mayan cichlids and may have caused slower growth than in Mexican populations. Third, the seasonal length frequencies of Martinez-Palacios and Ross (1992) were insufficient to accurately identify older year classes. Because growth slows with age, the length-frequency of cohorts corresponding to older age classes can overlap significantly, resulting in erroneously lower age estimates. Future efforts to age Mayan cichlids in Mexico should include thin-sectioned otoliths to evaluate the findings of Martinez-Palacios and Ross (1992).

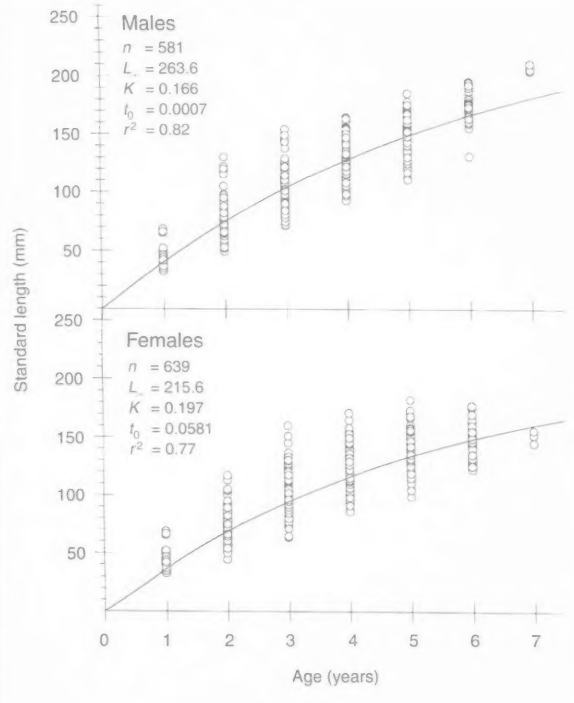

Figure 5

Observed and predicted lengths at age for male and female Mayan cichlids from the von Bertalanffy growth model. n=observed and back-calculated size-at-age information from 148 males and 157 females.

Although the Mayan cichlid has proliferated for over a decade in the natural and man-made habitats surrounding the Everglades, studies are only recently becoming available (e.g. Trexler et al., 2000). More introduced fish species are found in Florida than in any other state in the United States, and 13 of the 18 species with established populations are cichlids (Shafland, 1996). The impact of exotic species on native Florida fishes has been debated: Shafland (1996) proposed no demonstrable effect on native fishes, whereas Courtenay (1997) argued that lack of available data precludes a determination. Trexler et al. (2000) provided empirical data that support Shafland (1996), concluding that although exotics have been credited with native species extinctions in other ecosystems, native Florida fishes are not specialized or restricted to certain habitats and thus are able to cope with the invasion of exotics. Finding no drastic changes in the native ichthyofauna does not necessarily mean that exotic species do not affect indigenous fishes. Exotic species can introduce

numerous stresses not easily quantified, e.g. nest predation, direct predation, and competition for space (Trexler et al., 2000; senior author, unpubl. data). These stresses may affect the population dynamics of native fishes by altering their growth rate, increasing mortality, or decreasing reproductive success. During 1990–99, the Mayan cichlid population underwent a cyclical "boom and bust" pattern of yearly abundance typical of invasive species (Trexler et al., 2000). Why these patterns occur requires a better understanding of the parameters of reproduction, growth, and mortality that drive the population dynamics of this species. The presence of the Mayan cichlid in the Everglades and Florida Bay estuary warrants further research and monitoring efforts in the region to firmly understand the life history of exotics, native fishes, and their role in the ecosystem.

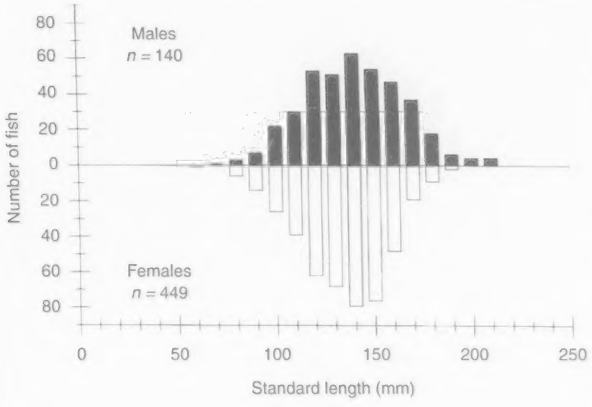

Figure 6

Length-frequency histograms for male and female Mayan cichlids collected with hook-and-line gear.

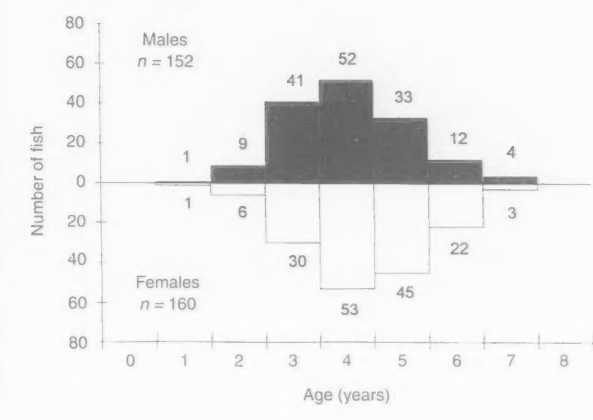

Figure 7

Age-frequency distributions for male and female Mayan cichlids collected with hook-and-line gear. Numbers indicate sample size.

Acknowledgments

We would like to thank Roy Crabtree, Daniel Merryman, Connie Stevens, and Rich McBride for their assistance. Ron Taylor and Mike Murphy shared their technical expertise with us, and with their editorial suggestions, Joe Serafy, two anonymous reviewers, and John Merriner greatly improved the manuscript. This project was funded by the U.S. Army Corps of Engineers through cooperative agreement 970092 between Everglades National Park and the National Audubon Society.

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Population status, seasonal variation in abundance, and long-term population trends of Steller sea lions (*Eumetopias jubatus*) at the South Farallon Islands, California*

Kelly K. Hastings
William J. Sydeman
Point Reyes Bird Observatory
4990 Shoreline Highway
Stinson Beach, California 94970
Present address (for K. K. Hastings): Alaska Department of Fish and Game
Division of Wildlife Conservation
333 Raspberry Rd.
Anchorage, Alaska 99518
E-mail address (for K. K. Hastings): kelly_hastings@fishgame.state.ak.us

Abstract–We examined seasonal and annual variation in numbers of Steller (northern) sea lions (*Eumetopias jubatus*) at the South Farallon Islands from counts conducted weekly from 1974 to 1996. Numbers of adult and subadult males peaked during the breeding season (May–July), whereas numbers of adult females and immature individuals peaked during the breeding season and from late fall through early winter (September–December). The seasonal pattern varied significantly among years for all sexes and age classes. From 1977 to 1996, numbers present during the breeding season decreased by 5.9% per year for adult females and increased by 1.9% per year for subadult males. No trend in numbers of adult males was detected. Numbers of immature individuals also declined by 4.5% per year during the breeding season but increased by 5.0% per year from late fall through early winter. Maximum number of pups counted declined significantly through time, although few pups were produced at the South Farallon Islands. The ratio of adult females to adult males averaged 5.2:1 and declined significantly with each year, whereas no trend in the ratio of pups to adult females was discernible. Further studies are needed to determine if reduced numbers of adult females in recent years have resulted from reduced survival of juvenile or adult females or from changes in the geographic distribution of females.

Manuscript accepted 1 August 2001.
Fish. Bull. 100(1):51–62 (2002).

Steller sea lions (*Eumetopias jubatus*) range from southern California along the West Coast of North America through the Aleutian and Pribilof Islands to the Kuril Islands and Okhotsk Sea, Japan (Kenyon and Rice, 1961). Major haulouts and rookeries have historically been centered at the Aleutian Islands and at islands and mainland sites around the Gulf of Alaska, where over 70% of the world population was located in the 1950s and 1960s (Loughlin et al., 1984). In 1990, the species was listed as threatened throughout its range under the Endangered Species Act owing to declines of over 50% from an estimated world population of 240,000–300,000 in the early 1960s to 116,000 individuals in 1989 (Loughlin et al., 1992). Numerically the decline was most severe in the western Gulf of Alaska where 50–80% declines occurred (Loughlin et al., 1992). Reduced juvenile survival appears to be the proximate cause for the decline (York, 1994); ultimate causes, however, are unknown. Effects of long-term environmental change and pollutants on Steller sea lions, and interactions or competition of these sea lions with commercial fisheries are potential contributing causes of this decline (NMML[1]).

In contrast to rookeries in the western Gulf of Alaska, southeast Alaska rookeries have increased by more than 60% over the past three decades (Loughlin et al., 1992). Based on differences in population trends and genetics (Bickham et al., 1996), a distinction has been made between two separate stocks: 1) the eastern stock, ranging from southeast Alaska to California, and 2) the western stock, ranging from the Gulf of Alaska, Aleutian Islands, and Pribilof Islands to Russia (U.S. Federal Register 62:24345–24355). In 1997, the National Marine Fisheries Service listed the western stock as endangered, whereas the eastern stock remained listed as threatened. However, differences in trends between rookeries in southeast Alaska and those in Canada, Oregon, and California may indicate that these areas deserve separate management considerations.

For example, rookeries in Canada and California suffered 40% and 80% declines respectively, from the early 1900s to 1970 (Bigg, 1988; Ainley et al.[2]); declines continued over the past

* Contribution 790 of the Point Reyes Bird Observatory, Stinson Beach, CA 94970.

[1] NMML (National Marine Mammal Laboratory). 1995. Status review of the United States Steller sea lion (*Eumetopias jubatus*) population. Report of the National Marine Mammal Laboratory, National Marine Fisheries Service, Seattle, WA, 61 p. [Available from National Marine Mammal Laboratory, 7600 Sand Point Way N.E., Seattle, WA 98115-0070.]

[2] Ainley, D. G., H. R. Huber, R. P. Henderson, and T. J. Lewis. 1977. Studies of marine mammals at the Farallon Islands, California, 1970–1975. Final report to the Marine Mammal Commission, Washington D.C. [NTIS publication number PB274046. Available from Point Reyes Bird Observatory, 4990 Stinson Beach, CA 94970.]

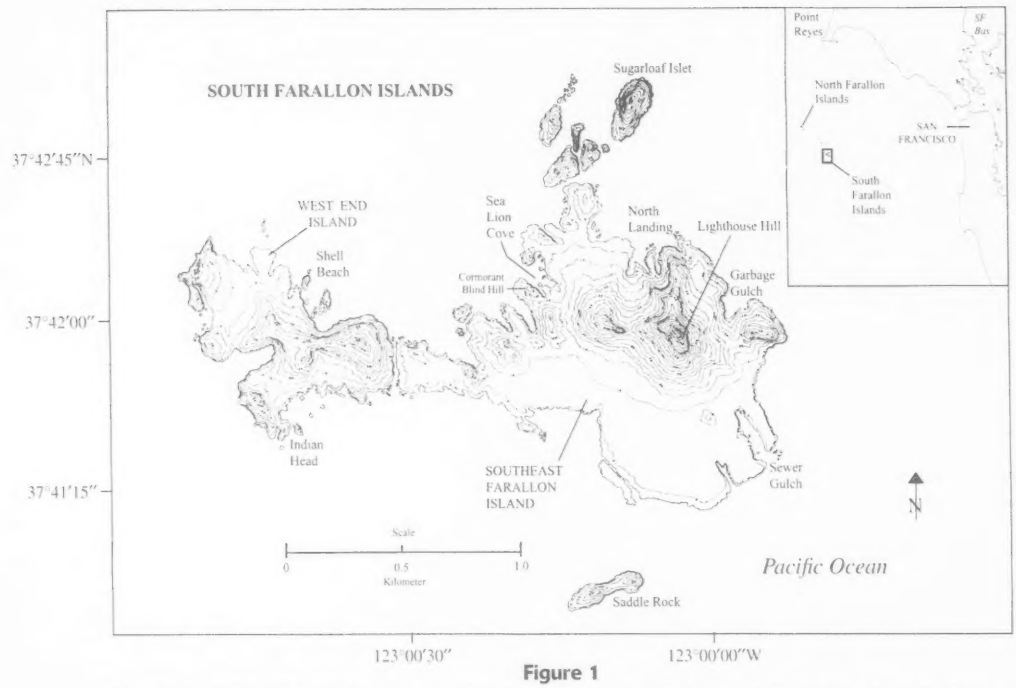

Figure 1

Map of the South Farallon Islands, including Southeast Farallon Island and West End Island. Steller sea lions were counted weekly from 1974 to 1997 from Lighthouse Hill, and several ground areas: North Landing, Cormorant Blind Hill, Sewer Gulch, and Garbage Gulch.

several decades at several California rookeries (Westlake et al., 1997; Sydeman and Allen, 1999; Le Boeuf et al.[3]). Whereas over 2000 Steller sea lions used the Channel Islands in the late 1930s, only 50 animals were observed there in 1959 (Bartholomew and Boolootian, 1960). Pupping at San Miguel Island, an historical rookery, has not been observed since 1981 (NMML[1]). Therefore to better understand patterns and causes of the population decline, trends and status of the eastern stock at southern rookeries deserve further investigation.

The Farallon Islands (37°42′N, 123°00′W), 40 km off the coast of San Francisco, California, are currently one of the most southerly haulout and breeding areas for Steller sea lions; Año Nuevo Island is the only rookery farther south. The Farallon Islands consist of three groups of islands: South Farallones (two islands, Southeast Farallon and West End, separated by a small surge channel), Middle Farallon (an intertidal rock), and North Farallones (four large sea stacks; Fig. 1). Although the status of Steller sea lions in California prior to 1800 was poorly documented, Steller sea lions bred at the Farallon Islands in the 1800s and early 1900s (Allen, 1880; Rowley, 1929) and were the most abundant sea lion in California and at the Farallon Islands from the early to mid 1900s (Rowley, 1929; Bonnot and Ripley, 1948). A large amount of data is now available to examine seasonal variation and long-term trends at the Farallon Islands from historical surveys conducted from 1927 to 1970 by the California Department of Fish and Game (CDFG; Bonnot and Ripley, 1948; Ripley et al., 1962; Carlisle and Aplin, 1971) and from surveys conducted weekly by Point Reyes Bird Observatory (PRBO) from 1971 to 1996. Although maximum numbers declined significantly from 1974 to 1997 for the total population (1.6% per year) and for adult females (3.6% per year; Sydeman and Allen, 1999), it is unknown whether numbers of other age classes also declined and in which seasons declines occurred. To understand proximate causes and consequences of the decline, several questions have yet to be addressed: have reduced pup production and reduced reproductive rates also occurred in recent years?; and what effect has the decline had on the adult sex-ratio? Finally, seasonal variation in counts for different sexes and age classes and variation in the seasonal pattern among years also have not been examined in detail at the Farallon Islands. The objectives of our study were to examine 1) seasonal variation in numbers among sexes and age classes; 2) trends in numbers from 1974 to 1996 by age class, sex, and season; and 3) averages and trends in pup production, reproductive rate, and adult sex-ratio.

[3] Le Boeuf, B. J., K. A. Ono, and J. Reiter. 1991. History of the Steller sea lion population at Año Nuevo Island, 1961–1991. Final report to National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, CA. Admin. report LJ9145C, 9 p. [Available from National Marine Fisheries Service, Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038.]

Methods

Survey methods

PRBO began conducting surveys of pinnipeds at the South Farallon Islands in 1971. In June 1973 surveys were standardized and all Steller sea lions visible on or in the water near the coast of the South Farallon Islands were counted weekly from standard vantage points on Southeast Farallon Island: 1) atop Lighthouse Hill (110 m) with binoculars or a 20–60× spotting scope, 2) from Cormorant Blind Hill (35 m) with binoculars, and 3) from North Landing, Sewer Gulch, and Garbage Gulch with no optical aids (Fig. 1). Most surveys were conducted between 1000 and 1800 hours on Thursdays if visibility was adequate. Beginning in 1977, animals were classified by age class (adult male, subadult male, adult female, immature, yearling, or pup) when possible, primarily by body size. Adult males were distinctive as very large animals with large muscular necks bearing well-developed manes of long, coarse hair on the chest, shoulders, and back. Subadult males were distinguished from adult males by their smaller size and less developed mane. Immature individuals included animals of distinctly smaller size, such as young-of-the-year (after November) and animals likely one to four years of age. The adult female category included animals smaller than subadult males but larger than immature individuals. Pups were distinguishable from June until late November by their thick, dark brown coats, which were later molted and replaced with a lighter brown coat after five to six months of age. Counts were conducted by numerous observers over the years; several observers conducted surveys for over a decade and all observers were trained in identification of sea lions by age class. Counts represent minimum estimates of numbers of sea lions hauled out because only 85% to 90% of the islands were visible from the study's vantage points.

We compared maximum counts taken during the breeding season (June–July) in recent years (1974–97) with counts from surveys conducted a single time during the breeding season (once annually) and intermittently over the years by CDFG from 1927 to 1970. From 1927 to 1938, counts of subadult or adult sea lions (i.e. excluding pups) made by at least two observers from boats were averaged (Bonnot, 1931, 1937; Bonnot et al., 1938). Methods of counting changed after 1938, such that counts after 1938 could only be compared cautiously with earlier years. Surveys were conducted by airplane, blimp, or boat in 1946 and 1947 and by airplane only from 1958 to 1970 (Bonnot and Ripley, 1948; Ripley et al., 1962; Carlisle and Aplin, 1971). Counts from 1946 to 1970 were likely overestimates because observers assumed that all sea lions north of Point Conception were Steller sea lions (many sea lions may have been California sea lions, *Zalophus californianus*) and because pups were likely included in these counts (Bonnot and Ripley, 1948; Ripley et al., 1962). Counts conducted by PRBO since the 1970s targeted only the South Farallon Islands, whereas CDFG counts included the South and North Farallon Islands. Monitoring of the North Farallon Islands since 1970, however, has been sparse. Although the North Farallon Islands are a known haulout area for Steller sea lions, pupping rates are unknown. The North Farallon Islands were surveyed during the breeding season by PRBO in 1977 (when 17 adult females and 1 pup were counted) and in 1983 (when 92 adults but no pups were counted; PRBO, unpubl. data[4]). Because of the exclusion of the North Farallon Islands in recent counts, comparisons with earlier CDFG data were made cautiously.

Under the direction of D. G. Ainley and H. R. Huber, pup production and pup mortality were monitored intensively from 1973 to 1986, when animals were breeding in accessible areas. Breeding areas were checked daily for new pups, and prematurely born and dead pups were noted. Breeding areas shifted from accessible to inaccessible areas over the years. From 1973 to 1975, all full-term pups were born on the more accessible Saddle Rock, a small islet one-quarter mile offshore (Fig. 1), and a few premature pups were born on the mainland. From 1976 to 1983, females pupped in the equally accessible Sea Lion Cove (Fig. 1), perhaps because of reduced disturbance on Southeast Farallon Island, although one pup was observed on Saddle Rock in 1981. Although photographs from the 1930s show large numbers of Steller sea lions on West End (Huber[5]), they were not observed there in recent years until 1983 (one female in the spring). The first pup was born on West End in 1985 (Huber[5]). Currently, the majority of the population is found and all pupping occurs at Indian Head and Shell Beach on West End (Fig. 1); both of these areas are inaccessible and difficult to monitor.

Statistical analyses

Statistical models have been developed that account for effects of observer, and environmental and survey-related covariates on counts of birds and marine mammals (Link and Sauer, 1997, 1998; Calkins et al., 1999; Frost et al., 1999; Forney, 2000). These models can increase accuracy in estimating and power in detecting population trends by reducing variability in counts and correcting biases in trend that result from methodological changes in survey design over time (such as changes in survey dates), particularly when few surveys are conducted during a standard survey window each year (Calkins et al., 1999; Frost et al., 1999). However, environmental covariates could not be included in the statistical models in our study when the full data set was used because observers recorded the times that surveys began and ended on only a few occasions prior to 1983 (41 of 569 surveys, or 7.2% of surveys), such that the majority of data during the first decade of the time series would be excluded. To include the entire

[4] PRBO (Point Reyes Bird Observatory). 1988. Unpubl. data. [Available from W. J. Sydeman, Point Reyes Bird Observatory, 4990 Shoreline Hwy, Stinson Beach, CA 94970.]

[5] Huber, H. R. 1985. Reproduction in northern sea lions on Southeast Farrallon Island, 1973–1985. Final report to the Gulf of the Farallones National Marine Sanctuary, San Francisco, CA, 22 p. [Available from Point Reyes Bird Observatory, 4990 Shoreline Hwy., Stinson Beach, CA 94970.]

time series, standard regression models, including survey date but excluding effects of environmental covariates, were used to examine seasonal patterns and trends. We believe the exclusion of other covariates during statistical modeling had little effect on trend estimates because surveys were conducted consistently over years and over the entire year interval, resulting in large sample sizes (n=1134 surveys conducted; range among years 1974–96: 45 to 52 surveys/year). It is unlikely that population trend estimates were confounded by changes in environmental conditions because no obvious annual trends in environmental conditions over the 22 years of the study (weather and tide data were collected daily [at 1000 hours] at Southeast Farallon Island) were apparent, except for a potential increasing annual trend in sea surface temperature (PRBO, unpubl. data[4]).

Seasonal abundance patterns To examine seasonal abundance patterns, polynomial regression (Kleinbaum et al., 1988) was used to fit a curve to counts pooled over years, 1974 to 1996. Data from 1971 to 1973 were excluded because survey methods were not standardized until the end of 1973. We fitted the regression model by first converting Julian date to orthogonal polynomial variables (linear combinations of the natural polynomial variables that contain the same information as the natural polynomial variables but are uncorrelated to each other) to avoid problems of multicollinearity when using higher-order terms (Kleinbaum et al., 1988). Higher-order terms were then added sequentially until the last term was not significant in the model (forward stepwise procedure, P>0.05). We then added *year* as a variable to the model and tested the *year* × *date* interaction to determine if the seasonal pattern varied significantly among years. To examine seasonal patterns by sex and age class, polynomial regression curves were fitted separately to counts of adult females, males (adults and subadults pooled), and immature individuals as described above. We excluded surveys in which not all individuals were identified by sex and age class (i.e. all surveys before 1977).

Annual abundance trends Because high-order polynomial models were used to address seasonal haulout patterns, annual abundance trends were examined in a separate analysis to simplify results. Seasonal variability in abundance was accounted for in annual trend models by using residuals from the regression of *Julian date* on counts. Assuming exponential rates of change, we log-transformed ($\log_e$) the residuals (centered about the mean count) and regressed the transformed residuals against the variable *year*. Annual rates of change were calculated as $e^{\beta_{Year}} - 1 \times 100\%$, where β_{Year} is the regression coefficient for annual trend (Caughley, 1977). The following groups were analyzed: 1) all animals, by pooling data over all 12 months and sex and age classes; and 2) each sex and age class, by pooling over a) all months, and b) two periods when peaks in counts were observed for some age classes (the breeding [May–July] and late fall through early winter [September–December] seasons). Nonlinearity in trend was assessed by using orthogonal polynomials as described earlier in this article. Assumptions of the regression model were verified by visual inspection of residuals.

Trends in pup production, reproductive rate, and adult sex ratio during the breeding season We used linear regression to test if the decline in maximum pup counts during surveys presented in Sydeman and Allen (1999) was significant. We used only data after 1977, when counts by age class were conducted consistently. Only data from surveys conducted from June to July were included because during the fall, the ability to distinguish young-of-the year from immature individuals was difficult and because an influx of nonnative pups may have occurred. For example, in November 1978, five times the number of pups known to have survived the breeding season and an increased number of adult females were observed (PRBO, unpubl. data[4]). The origin of these young-of-the-year is unknown, but the nearest known pupping areas are Año Nuevo Island and the North Farallon Islands. Although Steller sea lions are present at Point Reyes, no pups have been observed there in the past two decades (Sydeman and Allen, 1999).

To examine averages and trends in adult sex ratio and reproductive rate, we used maximum counts of adult females, adult males, and pups during June and July in each year and linear regression to test for annual trends. Reproductive rate was calculated as the maximum count of pups divided by maximum count of adult females. Because not all pups born were observed during surveys, we increased the maximum count of pups by 57%, the average amount that maximum pup counts underestimated true pup production from 1973 to 1986 (range: 33–90% among years). This average was determined from unpublished data of pup production as determined from daily observations of breeding areas (Huber et al.[6]).

Results

Seasonal abundance patterns

When data from all sexes and age classes were pooled, the seasonal abundance pattern was bimodal; one peak in numbers occurred before and during the breeding season (April–July) and another peak occurred from late fall through early winter (October–December; Fig. 2A). The regression model was complex with significant date and higher-order terms (variables $date^2$ through $date^8$); all P<0.001; adjusted r^2=0.28, n=1134); the variable $date^9$ was not significant (P>0.65). Counts varied significantly with year (P<0.001) and the seasonal pattern varied significantly among years ($date$×$year$ through $date^8$×$year$; P<0.001; adjusted r^2=0.61). Total numbers during the peak

[6] Huber, H. R., D. G. Ainley, R. J. Boekelheide, R. P. Henderson, and T. J. Lewis. 1988. Annual and seasonal variation in numbers of pinnipeds on the Farallon Islands, California (Table 3). Final report to the National Marine Mammal Laboratory, National Marine Fisheries Service, Seattle, WA, 35 p. [Available from Point Reyes Bird Observatory, 4990 Shoreline Hwy., Stinson Beach, CA 94970.]

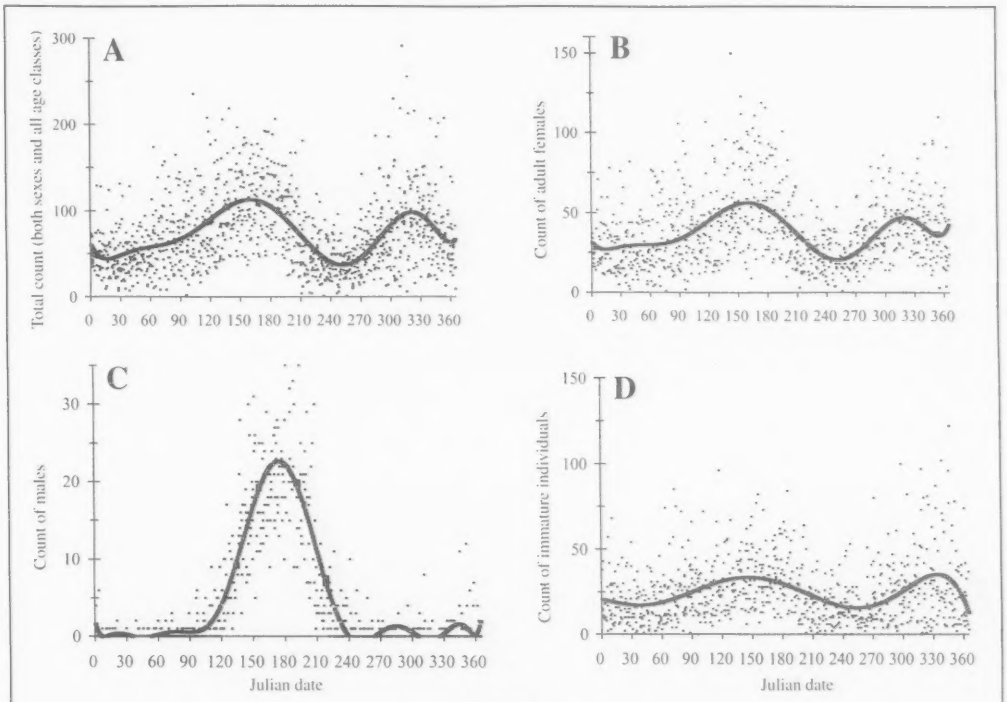

Figure 2

Seasonal variation in counts of Steller sea lions at the South Farallon Islands for (**A**) both sexes and all age classes; (**B**) adult females; (**C**) subadult and adult males; and (**D**) immature individuals and yearlings. Data from 1974 or 1977 to 1996 were pooled. Black dots indicate counts: black lines indicate predicted values from the regression model. Divisions on the *x*-axis approximate months. The best regression model for each group included the variables *date* and $date^2$ through (A) $date^8$ for total counts (adjusted r^2=0.28); (B) $date^8$ for adult females (adjusted r^2=0.22); (C) $date^{12}$ for males (adjusted r^2=0.77); and (D) $date^6$ for immature individuals (adjusted r^2=0.13).

breeding season averaged approximately 100 animals, ranging from 50 to 200 animals; whereas numbers from the late fall through early winter peak were more variable, averaging slightly less than 100 and ranging from less than 10 to 300 animals (Fig. 2A).

Seasonal patterns varied among sexes and age classes (Fig. 2, B–D). Counts of adult and subadult males peaked only during the breeding season (Fig. 2C), whereas counts of adult females and immature sea lions were bimodal (Fig. 2, B and D). When models including the variables *date* through $date^8$ were fitted to data for adult females and immature individuals separately, the seasonal pattern differed significantly between the two groups *(age class, year,* and all interaction terms: all $P<0.001$). Counts of immature sea lions were less peaked during the breeding season than those of adult females and, in contrast to the average adult female pattern, numbers during winter peaked on average slightly higher than during the breeding season (Fig. 2, B and D).

The seasonal pattern varied significantly among years for all age classes (*year* and *year*×*date* interactions for adult females and immature individuals: $P<0.001$, and for subadult and adult males: $P<0.05$). Variation in seasonal pattern among years was complex but several general patterns could be noted. A gradual shift in the peak breeding season count from the beginning of May in 1974 to the beginning to middle of June in 1979 was evident (Hastings and Sydeman[7]). The late fall–winter peak was very pronounced from 1984 to 1986, with maximum counts of 200 to 300 animals (Hastings and Sydeman[7]), most of which were immature individuals. From 1992 to 1996, the seasonal abundance pattern was muted with equal or higher numbers in the winter than in the breeding season (Hastings and Sydeman[7]).

[7] Hastings, K. K., and W. J. Sydeman. 1998. Status, seasonal variation and long-term trends in numbers of Steller sea lions, *Eumetopias jubatus*, at the South Farrallon Islands, California: 1927–1996. Final report to the National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, CA, 30 p. [Available from Point Reyes Bird Observatory, 4990 Shoreline Hwy., Stinson Beach, CA 94970.]

Table 1

Linear rates of change in counts of Steller sea lions on the South Farallon Islands by season, sex, and age class. Rate of change per year was calculated by 1) removing the effect of date on counts (i.e. by using residuals from regression of date on counts), and 2) log-transforming ($\log_e$) the sum of the residuals added to the mean count. * indicates significant trends ($P<0.05$) from regressions. n = sample size.

Age class	% change	β_{Year}	SE (β_{Year})	P	n
All animals					
All months	–0.44	–0.0044	0.0027	0.03*	1134
Adult females					
All months	–3.16	–0.0321	0.0032	<0.001*	866
Breeding season (May–Jul)	–5.89	–0.0607	0.0081	<0.001*	217
Late fall through early winter	2.50	0.0247	0.1637	0.80	280
Males (breeding season)					
All males	1.12	0.0111	0.0050	0.03*	217
Bulls	0.16	0.0016	0.0022	0.63	217
Subadult males	1.94	0.0192	0.0086	0.03*	217
Immature sea lions					
All months	0.55	0.0055	0.0019	0.004*	866
Breeding season	–4.51	–0.0461	0.0168	0.007*	217
Late fall through early winter	4.97	0.0485	0.0078	<0.001*	280

Annual abundance trends

Although visual inspection showed that residuals of log-transformed counts were not normally distributed, a square-root transform of counts normalized residuals. We report trend estimates from log-transformed counts because results of statistical tests for trends with log- and square-root-transformed data were identical.

After removing seasonal effects (i.e. residuals from regression of *date* on count were used), all sexes and age classes showed significant trends but in different directions (Table 1). When data from all sexes and age classes were pooled, the trend was complex (variables *year* through *year*^{3}: all $P<0.05$; n=1134; Fig. 3A). Counts were highest in the late 1970s to early 1980s and declined only slightly during the late 1980s to early 1990s. A slight (–0.4% per year) linear decrease in total counts (pooling over months, sexes, and age classes) with *year* was significant ($P<0.05$; Table 1). Adult female counts declined significantly although the rate of decline slowed in recent years (variables *year* and *year*^{2}: $P<0.01$; n=866; Fig. 3B). Counts of adult females declined significantly during the breeding season (variables *year* and *year*^{2}: $P<0.01$; n=217; Fig. 3B), whereas no trend during late fall and early winter was evident (P=0.80; Table 1). Linear rate of decline for adult females was –3.2% per year for all months combined and –5.9% per year during the breeding season (both $P<0.001$; Table 1).

In contrast, numbers of males during the breeding season increased linearly with *year* at a rate of 1.1% per year ($P<0.05$; n=217; Table 1). This increase was due to an increased number of subadult males (1.9% per year; $P<0.05$; Table 1; Fig. 3C), whereas the numbers of adult males were stable ($P>0.60$; Table 1). Counts of immature individuals also increased slightly (0.6% per year; Table 1) but significantly when counts from all months were pooled (variables *year* and *year*^{2}: $P<0.01$; n=866; Fig. 3D). The increase was due to the greater numbers of immature individuals from late fall through early winter in recent years (linear trend=5.0% per year, Table 1; *year* and *year*^{2}: $P<0.01$; n=280; Fig. 4D). However, numbers of immature individuals present during the breeding season declined at a rate of –4.5% per year (Table 1; *year*: $P<0.01$; n=217; Fig. 3D).

Trends in pup production, reproductive rate, and adult sex ratio during the breeding season

Maximum pup count from surveys declined significantly from the mid-1970s to the mid-1980s from 15 to 2–4 pups and has remained low in recent years (*year* and *year*^{2}: $P<0.003$; Fig. 4). After adjusting for pups not seen during surveys, reproductive rates of adult females ranged from 2.0% to 21.2% among years, with an average rate of 10.7% (Fig. 4). Although reproductive rate appeared to decline in the 1980s and recovered to 1970s levels in the 1990s, no trend was discernible (*year* and higher-order terms: $P>0.20$; Fig. 4). The ratio of adult females to adult males during the breeding season ranged among years from 10.3:1 to 1.8:1, with an average of 5.2:1 (Fig. 4). The ratio of adult females to adult males declined significantly and linearly with *year* ($P<0.001$).

Discussion

Although the Farallon Islands are an important haulout area for Steller sea lions in California, numbers of ani-

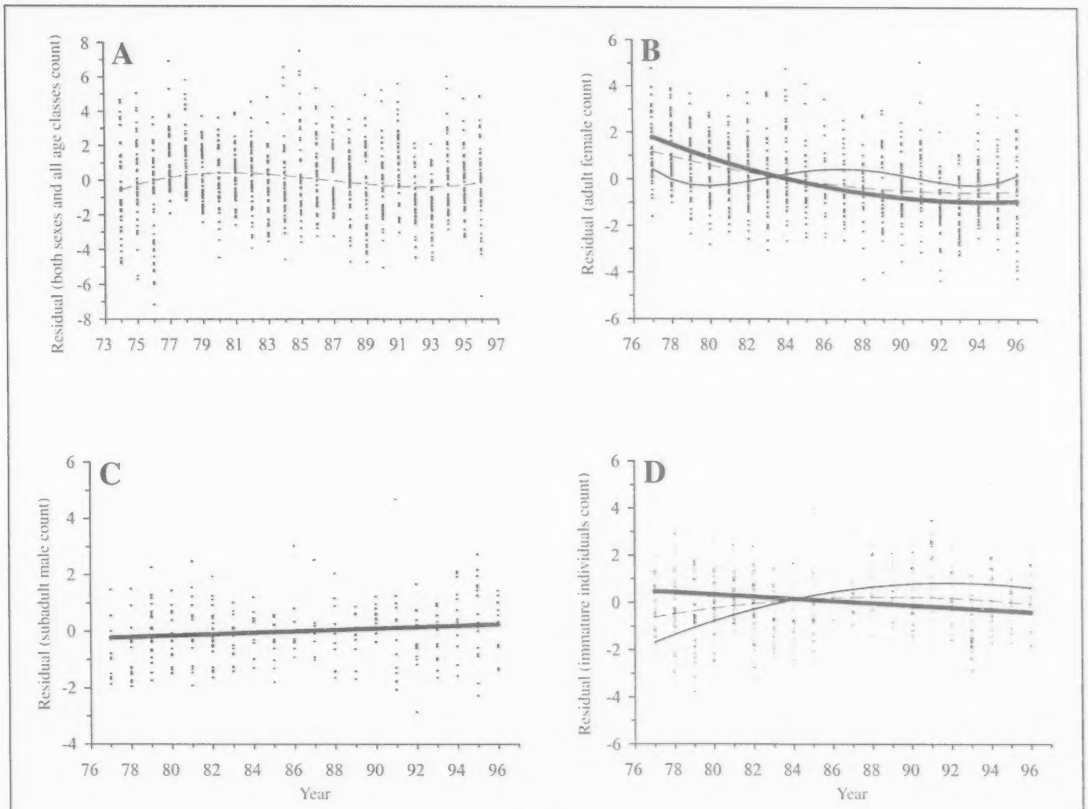

Figure 3

Annual trends in counts of Steller sea lions at the South Farallon Islands from 1974 or 1977 to 1996 for (**A**) both sexes and all age classes; (**B**) adult females; (**C**) subadult males; and (**D**) immature individuals and yearlings. Significant trends in counts, after accounting for survey date (residual centered about the mean count from Figure 2, square-root transformed), are shown for: all months (light dashed line); only counts during the breeding season (May – July; solid black line); and only counts from late fall through early winter (September–December; solid light black line). Results of significance tests using square-root and $\log_e$-transformed counts were identical; Linear rates of change from $\log_e$-transformed counts are shown in Table 1.

mals at the Farallon Islands are currently lower (0.06 of the 1989 statewide count, 0.09 of the count from four major sites) than at the other three major California sites (Año Nuevo Island, St. George Reef, and Sugarloaf Island) which ranged from 0.16 to 0.18 of the 1989 statewide count, and from 0.26 to 0.37 of the count from four major sites (Loughlin et al., 1992). A smaller proportion of the statewide Steller sea lion population has used the Farallon Islands in recent years, compared with population counts in the 1927–30 data, when Farallon animals accounted for 0.11 to 0.14 of the statewide count (Bonnot and Ripley, 1948). Historical pup production at the Farallon Islands is unknown, but both the Farallon Islands and Año Nuevo Island were identified as the two largest and most important Steller sea lion rookeries in the state in the early 1920s (Rowley, 1929). Pup production at the South Farallon Islands over the past two decades has been very low at <30 pups per year and in the last 10 years, at <10 pups per year. Pup production since the mid-1980s, however, may be underestimated owing to the reduced probability of sighting pups since 1984 when pupping areas shifted to West End Island, which is farther away from the survey vantage points. Pup production at other major sites in California included 117–137 pups at Sugarloaf Island and Cape Mendocino in the early 1980s, 115 pups at St. George Reef in 1994, and 230–243 pups at Año Nuevo in 1993–94 (Westlake et al., 1997; NMML[1]).

Reproductive rates of Steller sea lions at the South Farallon Islands were also low; an average of only 0.11 of females present during the breeding season produced pups. This number may be biased low because some immature males may have been included in the adult female count. This ratio is much lower than that for rookeries in British Columbia (>0.70, Pike and Maxwell, 1958), Año Nuevo, California (average of 0.40 to 0.50 from 1962–1990; Le Boeuf et al.[3]) and Ugamak Island, Alaska, where ratio of

pups to females increased from 0.75 to >1.00 from 1968 to 1986 (Merrick et al., 1987). The South Farallon ratio is more typical of peripheral areas of rookeries in Alaska where only 0.01 to 0.09 of females had pups compared with main areas of rookeries where ratios averaged 0.63 to 0.74 (Withrow, 1982).

Similarly, high pup mortality rates observed at the Farallon Islands (average of 0.49 of pups born from February to August, range of 0.33 to 0.90 among years; Huber et al.[6]) are more characteristic of peripheral areas of rookeries where pup mortality ranged from 0.30 to 1.00 compared with 0.10 to 0.12 at main rookery sites (Withrow, 1982). Rookeries had much lower pup mortality rates during the first two months of life than those observed at the Farallon Islands, including Año Nuevo Island, California (0.10, Gentry, 1970), and sites in Alaska (0.03–0.14, Merrick et al., 1987). The frequency of premature pupping (0.40 of those born; Huber et al.[6]) is also very high compared with the frequency at rookeries in Alaska (0.09; Pitcher and Calkins, 1981), Oregon (0.04; Mate, 1973), at Año Nuevo Island (0.02; Gentry, 1970). As at Año Nuevo, most premature pups are born from February to May at the Farallon Islands (0.65 born in April with a range of February to May), whereas full-term pups are born from mid-May to late July (Gentry, 1970; Huber[5]). Causes of the high rate of premature pupping at the Farallon Islands are unknown but may be due to several factors known to cause reproductive failure in pinnipeds, including disease or exposure to pollutants (Gilmartin et al., 1976; Huber[5]), or a prevalence of young, inexperienced, or malnourished females (Pitcher et al., 1998). A high frequency of abortions has been observed at haulout sites rather than at rookeries in Alaska (Pitcher and Calkins, 1981). Low pup production and reproductive rates, coupled with high pup mortality and premature pupping rates, support characterization of the Farallon Islands in recent years as a haulout site or peripheral rookery for this species.

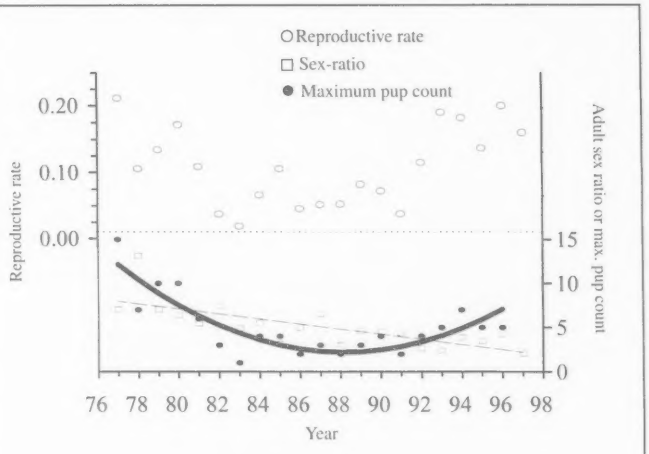

Figure 4

Annual variation in reproductive rate, adult sex ratio, and maximum pup count during the breeding season (June–July) at the South Farallon Islands, 1977–97. Reproductive rate was defined as the maximum pup count divided by the maximum count of adult females per year. Adult sex ratio was calculated as the maximum number of adult females divided by the maximum number of adult males (bulls) counted per year. Significant ($P<0.05$) trends are shown for adult sex ratio (dashed black line) and maximum pup count (bold black line).

Seasonal patterns in counts

Seasonal haulout patterns varied significantly among sexes and age classes. Adult and subadult male attendance was highly seasonal and males were present only during the breeding season. In contrast, adult females and immature individuals were present year-round and their numbers peaked twice (breeding season and from late fall through early winter). Many studies reported the absence of adult and subadult males at California rookeries outside the breeding season, including Año Nuevo Island (Orr and Poulter, 1967) and San Miguel Island (Bartholomew, 1967), and the presence of females and immature individuals at rookeries year-round (Rowley, 1929; Bartholomew, 1967). At Canadian rookeries, males were also generally absent in the winter, but small numbers of females and young of the year usually remained at rookeries throughout the year (Bigg, 1988). Circumstantial evidence suggests males from California migrate northward or males from Southeast Alaska move southward in winter, or both movements take place. Large numbers of males have been seen outside the breeding season off northern California (Fry, 1939), Oregon, Washington (Mate, 1973), and southern Vancouver Island (Bigg, 1988). Total numbers of Steller sea lions are also higher in the winter than in the summer off the Canadian coast (Bigg, 1988); some winter haulouts in Canada consist almost exclusively of males (Bigg, 1988). The earliest evidence for sea lion migrations was provided by the recovery of north-coast native American spearheads from several sea lions killed off southern California in the late 1800s; and in June 1870, a spearhead used by native Alaskans was found in a large male sea lion at Point Arena, California (Scammon, 1874). Seasonal northward movement has also been documented in male California sea lions, which were similarly absent from southern sites outside the breeding season but which ranged up into Washington and British Columbia during winter (Starks, 1921; Fry, 1939; reviewed by Bartholomew, 1967).

In contrast to animals on the Farallon Islands, animals of all age classes and both sexes on Año Nuevo Island were present in significant numbers only during the breeding season from 1967 to 1990 (Le Boeuf and Bonnell, 1980; Le Boeuf et al.[3]). Data from 1962 and 1963 indicated a substantial presence of Steller sea lions at Año Nuevo through the fall and winter (Orr and Poulter, 1965) and therefore the lower numbers and, more recently, near absence of all

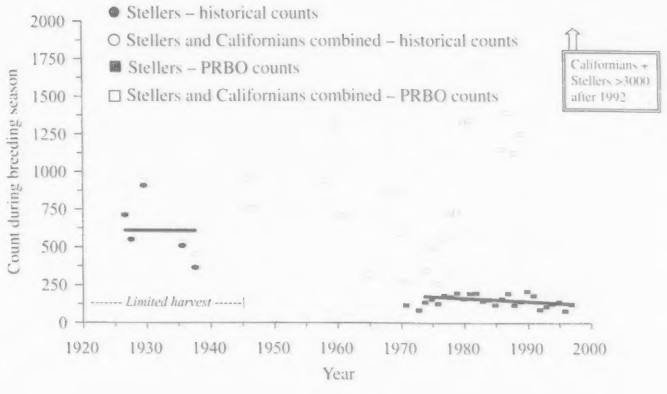

Figure 5

Counts of sea lions at the Farallon Islands during the breeding seasons, from 1927 to 1997. Historical counts, 1927–38: total count from single census per year conducted by boat; includes North and South Farallones and adults and subadults only (Bonnet et al., 1938). Historical counts, 1946–70: total count from a single census conducted each year by airplane, blimp, or boat; includes North and South Farallon Islands and may include pups, subadults and adults. Steller and California sea lions were not distinguished during these surveys. Instead all sea lions north of Point Conception were considered Steller sea lions and those south of Point Conception were considered California sea lions (Bonnot and Ripley, 1948; Ripley et al., 1962; Carlisle and Aplin, 1971). Point Reyes Bird Observatory counts, 1974–97: maximum total counts during June and July from weekly censuses at South Farallon Islands only (North Farallones excluded); includes pups, immature individuals, subadults, and adults. Means or trends over years are shown for Steller counts only (solid black lines) and for counts of Steller and California sea lions combined (dashed lines).

age classes after the breeding season may be a recent phenomenon. Similarly, Steller sea lions of various sexes and age classes were present off Humboldt County, California, only from mid-April to September (Sullivan, 1980).

Diverse seasonal patterns among sites were also evident in Canada and Alaska. In Canada, animals were usually present year-round on rookeries and numbers peaked during July, whereas year-round haulouts showed no marked seasonal variation and a variety of sexes and age classes were present in winter (Bigg, 1988). Winter haulouts were occupied only in the winter and consisted of either only males or a variety of sexes and age classes (Bigg, 1988). In Alaska, many rookeries were abandoned and some haulouts were occupied only in winter; other haulouts and rookeries were occupied year-round (Kenyon and Rice, 1961; NMML[1]). Major seasonal shifts in distribution were not evident in Alaska, although winter counts were substantially lower than summer counts and there was a greater proportion of animals at haulouts than at rookeries in winter (NMML[1]). The diversity in seasonal patterns observed among sites (including rookeries and haulouts) in California and elsewhere has confounded generalizations concerning seasonal haulout patterns, although a general shift from rookeries to haulouts in winter seems to occur throughout most of the species range.

Population status of Steller sea lions in southern and central California

Decline from historical numbers Substantial declines in Steller sea lions at the Farallon Islands have been evident since the 1920s and in recent decades. Numbers declined approximately 75–80% from an average of 600–790 animals from 1927 to 1947 to an average of 150 animals (maximum count) from 1974 to 1997 (Fig. 5). This decline may be overestimated because animals on the North Farallon Islands have not been included in surveys since 1970 and because more animals are likely visible by boat or air than from island-based vantage points (Westlake et al., 1997). However, 85% to 90% of the island is visible from vantage points and therefore effects of incomplete coverage should be small. Although the decline in numbers was severe between 1938 and 1974, the rate of decline cannot be determined for this period because surveys from this period did not distinguish Steller from California sea lions (Fig. 5). These surveys assumed that all sea lions north of Point Conception were Steller sea lions and that all sea lions south of Point Conception were California sea lions (Carlisle and Aplin, 1971). Assessing the status of Steller sea lions from the 1946–70 CDFG counts has been confounded by growth in the California sea lion population

over the same period. For example, California sea lions made up only 20% of the total sea lion count at the Farallon Islands in 1938 (Bonnot and Ripley, 1948); but by the mid 1970s, California sea lions were twice as numerous as Steller sea lions during June and July (Fig. 5).

The role of commercial harvest and direct take or harassment of sea lions by humans in this decline is uncertain. Large numbers of sea lions were hunted in California in the late 1800s for oil, hides, and "trimmings" (which included the whiskers, genitalia, and gall bladder of adult males) that were sold to Chinese markets (Scammon, 1874). Hunting sea lions for oil became unprofitable around 1900 because of the reduction in sea lion numbers and the wide-spread availability of petroleum products (Rowley, 1929). A reduced sea lion harvest for hides, trimmings, and (in Mexican waters) pet food, continued until the end of the 1930s when Chinese markets disappeared with the onset of the Japanese-Chinese war and protests were successful in stopping Mexican harvests (Bonnot, 1951). During the same period, although fewer sea lions were taken by sportsman, fisherman, and collectors for museums and zoos, rookery abandonments and population declines still persisted in Oregon and southern California (Rowley, 1929; Bonnot, 1931). An additional cause for these population declines may have been the sea lion hunts that were introduced by commercial fisheries around 1900 to reduce competition for fish (Bonnot, 1937). For example, a bounty was offered for Steller sea lions in the early 1900s in areas north of California (Rowley, 1929; Bonnot, 1931; Bonnot, 1951).

Although numbers harvested in California are not well documented and the role of harvest in the decline is not obvious, several arguments can be made that declines in Steller sea lions from the 1940s to 1970s were likely not due to effects of harvest alone. During the period of commercial harvest, Steller numbers appeared stable (Bonnot and Ripley, 1948), whereas the 75–80% decline was evident after 1947, after commercial hunting and collections had ended, although harassment by fisherman continued. After 1947, the California sea lion population increased exponentially throughout the state from 3050 in 1947 to a minimum of 18,047 in 1970 (Bonnot and Ripley, 1948; Carlisle and Aplin, 1971), whereas numbers of Steller sea lions on the Channel Islands and at the Farallon Islands declined from 80% to 100% during this period. Large increases in California sea lions were evident after commercial harvesting ended, even though many more California than Steller sea lions were likely hunted commercially, poached, or captured because of difficulty hunting in the steep, rocky intertidal areas frequented by Steller sea lions (Rowley, 1929; Bonnot, 1951). This reasoning suggests that factors in addition to harvest have influenced the population decline. Proposed causes include reduction of the prey base due to overexploitation by commercial fisheries (Ainley and Lewis, 1974), shifts in prey composition due to ocean warming, and competition for food with growing numbers of California sea lions (Bartholomew, 1967).

Human disturbance, however, likely played some role in the decline, in respect of which Steller sea lions may be more affected by human disturbance than California sea lions. For example, the large Steller sea lion rookeries at San Miguel Island and at Seal Rocks, just off San Francisco, were abandoned permanently because of harassment and shooting by hunters for sea lion trimmings or by fisherman (Rowley, 1929). Southeast Farallon Island was inhabited by fair numbers of lighthouse keepers and their families (since the mid-1800s) and egg hunters (men collecting seabird eggs for sale in commercial markets for human consumption) from the mid-1800s to the mid-1900s. Highest human occupancy occurred during World War II, when over 50 military personnel were added to the island's population (Ainley and Lewis, 1974). Families were removed in 1965 and the lighthouse was automated in 1972, after which time only PRBO researchers remained on the island (Ainley and Lewis, 1974). Despite the designation of the North and Middle Farallon Islands in 1909 and the South Farallon Islands in 1969 as a national wildlife refuge, harassment by fisherman and disturbance from low-flying helicopters was common into the 1970s (Ainley and Lewis, 1974). Heightened human presence in the mid-1900s likely increased the abandonment of Steller sea lions from the islands during the period of dramatic decline.

Recent population trends Over the last 20 years, the numbers of Steller sea lions on the South Farallon Islands has continued to decline significantly. Numbers of adult females present during the breeding season declined by 5.9% per year from 1977 to 1996, although the rate of decline has lessened since the mid to late 1980s (Fig. 3B). This rate of decline is much higher than the 3.6% per year decline reported for adult females by Sydeman and Allen (1999), who used maximum counts and data from all seasons, although rates are similar between the two studies when similar data were used (3.2% per year estimated from our study, when data from all seasons were pooled). These findings demonstrate the importance of accounting for seasonal effects when investigating population trends. The rate of decline of 5.9% per year is similar to the rate of decline observed during the breeding season in the area of greatest decline in Alaska (from Kiska Island to the Kenai Peninsula), where rates of decline varied from approximately 5% (1975–85 and 1990–94) to 16% (1985–90; York et al., 1996).

Numbers of immature individuals present during the breeding season have also declined by 4.5% per year over the past several decades, but an overall net increase in immature individuals on the islands has been apparent owing to increased numbers in the late fall and early winter. Numbers of immature individuals on the Farallon Islands in the winter were particularly high from 1984 to 1986. Immature individuals have continued to be present in significant numbers during winter in recent years. It is uncertain where these young animals originated from, but overall declines in juvenile counts, coupled with significant declines in juvenile counts during the breeding season, suggest that increased numbers in winter may represent changes in movement and haulout patterns of juveniles rather than improved juvenile survival in recent years. Increased numbers of subadult males hauled out on the South Farallon Islands during the breeding season in

recent years may have resulted from increased emigration or movement of subadult males from Año Nuevo Island due to increased competition for the declining number of females there. A stable number of adult males, coupled with declines in numbers of adult females, has resulted in a significant reduction in the adult male-to-female ratio on the South Farallon Islands during the breeding season in recent years.

These results demonstrate that reduced numbers of Steller sea lions on the Farallon Islands in recent years have been driven by reduced numbers of adult females during the breeding season, although reproductive rate and pup mortality rate were stable at this peripheral rookery. Patterns were similar at Año Nuevo, where there were sharp declines in numbers of females and pups during the breeding season but where no trend in reproductive rate was apparent from 1962 to 1990 (Le Boeuf et al.[3]). However, unlike the Farallon Islands, number of males at Año Nuevo during the breeding season also declined sharply during the same time period (Le Boeuf et al.[3]). Although the rate of decline at the Farallon Islands has lessened in recent years, large declines of 9.9% per year for pups and 31.5% per year for older animals may have occurred at Año Nuevo from 1990 to 1993, when negative effects of the 1992 El Niño may have affected estimates from this short time series (Westlake et al., 1997).

It is unknown whether reduced numbers of adult females and immature individuals present during the breeding season have resulted from reduced survival or changes in geographic distribution. Because significant declines in Steller sea lions from historical numbers and over the past several decades have occurred at San Miguel Island, Año Nuevo Island, and the South Farallon Islands, greater monitoring and protection by state or federal agencies of the southern populations are warranted. Estimates of age-class specific survival rates of females are needed to determine if reduced numbers of females are due to increased juvenile or adult mortality. More intensive studies tracking individual Steller sea lions in California are required to determine if declining numbers indicate a northward shift in the breeding range and to document migratory movements of males and females. Population dynamics and movements of prey of Steller sea lions, dietary overlap with California sea lions, and interactions of sea lions with commercial fisheries in California must be examined to determine natural and anthropogenic causes for changes in sea lion numbers or distribution.

Acknowledgments

H. R. Huber deserves special recognition for her contributions during the early years of our study. Financial support for manuscript preparation was provided by the National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Science Center under contract 40JGNF600336 to W. J. Sydeman. The Friends of the Farallones, Homeland Foundation, Roberts Foundation, Bradford Foundation, and Exxon Corporation also provided funds for data preparation and fieldwork. We are particularly grateful to D. G. Ainley for initiating pinniped studies on the Farallon Islands in 1971. We also sincerely thank Nadav Nur and Grey Pendleton for statistical advice and reviews of the manuscript. We also thank the many observers who have conducted surveys over the past three decades: D. Ainley, G. Ballard, B. Boekelheide, H. Carter, S. Emslie, P. Henderson, M. Hester, H. Huber, S. Johnston, J. Lewis, E. McLaren, S. Morrel, J. Nusbaum, J. and T. Penniman, P. Pyle, T. Schuster, J. Walsh, and others. General studies of marine mammals at the South Farallon Islands have been graciously supported over the years by the Marine Mammal Commission, U.S. Fish and Wildlife Service (USFWS), and the Gulf of the Farallones National Marine Sanctuary. In particular, USFWS and the San Francisco Bay National Wildlife Refuge have provided 28 years of financial, logistical, and moral support; to those involved, we offer sincere gratitude. We also thank the Farallon Patrol for transport to and from Southeast Farallon Island. Michael Rehburg assisted with creating the Farallon Island map. This manuscript benefited greatly by suggestions from Andrew Trites and several anonymous reviewers.

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Larval and settlement periods of the northern searobin (*Prionotus carolinus*) and the striped searobin (*P. evolans*)*

Richard S. McBride
Marine Field Station
Institute of Marine and Coastal Sciences
Rutgers University
800 Great Bay Blvd.
Tuckerton, New Jersey 08087
Present address: Florida Marine Research Institute
100 Eighth Avenue SE
St. Petersburg, Florida 33701-5095
E-mail address: richard.mcbride@fwc.state.fl.us

Michael P. Fahay
Sandy Hook Laboratory
Northeast Fisheries Science Center
National Marine Fisheries Service, NOAA
Highlands, New Jersey 07732

Kenneth W. Able
Marine Field Station
Institute of Marine and Coastal Sciences
Rutgers University
800 Great Bay Blvd.
Tuckerton, New Jersey 08087

Abstract—This study reports new information about searobin (*Prionotus* spp.) early life history from samples collected with a Tucker trawl (for planktonic stages) and a beam trawl (for newly settled fish) from the coastal waters of New Jersey. Northern searobin, *Prionotus carolinus*, were much more numerous than striped searobin, *P. evolans*, often by an order of magnitude. Larval *Prionotus* were collected during the period July–October and their densities peaked during September. For both species, notochord flexion was complete at 6–7 mm standard length (SL) and individuals settled at 8–9 mm SL. Flexion occurred as early as 13 days after hatching and settlement occurred as late as 25 days after hatching, according to ages estimated from sagittal microincrements. Both species settled directly in continental shelf habitats without evidence of delayed metamorphosis. Spawning, larval dispersal, or settlement may have occurred within certain estuaries, particularly for *P. evolans*; thus collections from shelf areas alone do not permit estimates of total larval production or settlement rates. Reproductive seasonality of *P. carolinus* and *P. evolans* may vary with respect to latitude and coastal depth. In this study, hatching dates and sizes of age-0 *P. carolinus* varied with respect to depth or distance from the New Jersey shore. Older and larger age-0 individuals were found in deeper waters. These variations in searobin age and size appear to be the combined result of intraspecific variations in searobin reproductive seasonality and the limited capability of searobin eggs and larvae to disperse.

Manuscript accepted 30 July (2001).
Fish. Bull. 100:63–73 (2002).

Although adult fish assemblages offshore of the middle Atlantic states are fairly well known (e.g. Edwards, 1976; Colvocoresses and Musick, 1984; Gabriel, 1992), the early life history of many of these same species and the function of shelf habitats as nursery grounds are poorly understood (e.g. Fahay, 1983, 1993; Able and Fahay, 1998). Because year-class strength is believed to stabilize prior to the early juvenile stage, information about the transition from the plankton to benthic (i.e. settlement) habitats should contribute to our understanding of the population processes of benthic fishes (Cushing and Harris, 1973; Campana et al., 1989; Myers and Cadigan, 1993). Settlement is regarded as a dynamic period of early development because mortality rates can differ between pre- and postsettlement life stages (Sale and Ferrell, 1988), dramatic morphological and physiological transformations occur (Youson, 1988; Markle et al., 1992; McCormick, 1993), and behaviors become evident that allow for delaying settlement until suitable juvenile habitat is found (Cowen, 1991; Sponaugle and Cowen, 1994). Ultimately, an understanding of the life cycle of any benthic species is constrained if the settlement period is not viewed as an integral transition from the planktonic to the adult period.

Our study contributes to an understanding of how fishes use continental shelf habitats as nurseries with an examination of the early life history of the northern searobin, *Prionotus carolinus*, and the striped searobin, *P. evolans*. Both are common species in the coastal region between Cape Cod and Cape Hatteras, but relatively little is known about their early life history owing largely to their low economic importance in relation to the heavily exploited fisheries of this region (McBride et

* Contribution 2001-28 of the Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, NJ 08901.

al., 1998). Both species are known to begin spawning as early as May and to continue spawning into October as determined by maturity indices (e.g. Richards et al., 1979; Wilk et al., 1990). *Prionotus* spp. eggs and larvae are known to be seasonally abundant above the continental shelf and within some estuaries (e.g. Richards et al., 1979; McBride and Able, 1994) but eggs and larvae are difficult to identify to species on a routine basis. Therefore we took advantage of recently reported morphological information (Able and Fahay, 1998) to examine ichthyoplankton collections.

Our study was designed to examine how spawning patterns varied between two congeners, but intraspecific spawning variation also became evident. A second goal of our study was to examine settlement—to date not reported for either species. Both species undergo flexion and complete fin-ray development at about 6–8 mm SL (Yuschak and Lund, 1984; Yuschak, 1985; Able and Fahay, 1998). Separation of prehensile rays on the pectoral fin, a major adaptation for benthic feeding (Morrill, 1895; Bardach and Case, 1965; Finger and Kakil, 1985), occurs in fish as small as 12 mm SL (Yuschak, 1985). Yet settled juveniles <25 mm SL are rare (Lux and Nichy, 1971; Richards et al., 1979; McBride and Able, 1994), which raises the question of whether *Prionotus* spp. are competent to settle after completing fin-ray development or whether they commonly delay settlement. Using a novel combination of sampling gears, we collected a continuum of late larval and early juvenile *Prionotus* spp. to examine settlement directly. We report for the first time species-specific larval abundances, distributions, ages, sizes, growth rates, and descriptions of early benthic existence.

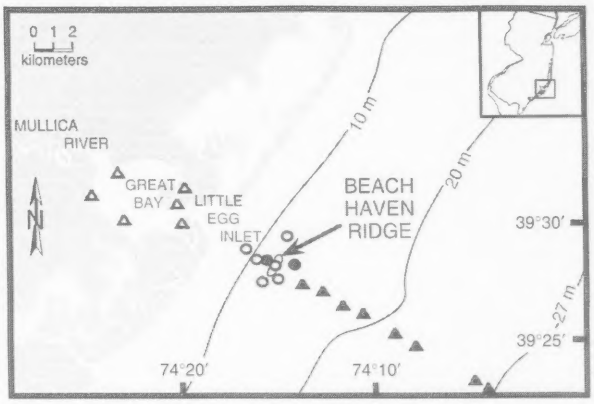

Figure 1

Map of sampling station locations in southern New Jersey, including the main stations at Beach Haven Ridge (landward and seaward: filled circles), other ridge stations (open circles), continental shelf transect stations (filled triangles), and estuarine stations (open triangles). The state of New Jersey, and the study location, are shown in the inset.

Materials and methods

Collections were made in coastal waters of New Jersey, specifically near Beach Haven Ridge (Fig. 1, Table 1), a prominent sand ridge formation that rises to about 8 m depth and is surrounded by depths of 14–16 m (Stahl et al., 1974). Sampling frequency at two stations, one landward and the other seaward of the ridge, was every two to six weeks from July 1991 to November 1992. Two tows of a Tucker trawl (1 m^2) were made at each station in a double, stepped-oblique fashion. One tow was made from the surface to the bottom (three minutes duration) and the other tow was fished from the bottom back to the surface (six minutes). Newly settled juveniles and older fishes were sampled with a 2-m beam trawl in Great Bay estuary, near Beach Haven Ridge, as well as in other habitats (Fig. 1). The data from these stations were arranged in the following groups: 1) the two principal ridge stations (described above); 2) miscellaneous stations scattered on top of and around the ridge; 3) stations along a transect leading directly offshore from the ridge; and 4) a cluster of stations within nearby Great Bay. Generally, three tows were completed at stations immediately landward and seaward of the ridge, but only two tows were completed at other stations. Beam trawl tows offshore of Little Egg Inlet took one minute to complete, but estuarine tows were reduced to 20 or 30 seconds to avoid collecting large volumes of macroalgae, detritus, shell, etc. Sampling occurred during daylight unless otherwise stated. Details of sampling procedures are provided by Hales et al.[1] Volume or area sampled was calculated by using a flow-meter for ichthyoplankton collections or a meter wheel for beam trawl collections. Larval density is presented as the geometric mean number of fish/m^3 for Tucker trawl collections. Juvenile density is presented as the geometric mean number of fish/m^2 of sea bottom. Calculations of geometric means follow Sokal and Rohlf (1981).

The standard length (SL) of all, or at least 20 fish per tow, was measured after the fish were preserved in 95% ETOH. The term "larva" was used in reference to individuals collected in Tucker trawl tows. Preflexion larvae were distinguished from flexion larvae by the absence or presence, respectively, of cartilaginous urals on the ventral edge of the notochord tip; the development of these urals accompanied flexion of the notochord tip (Kendall et al., 1984). Larvae were characterized as postflexion stage once the notochord tip moved anterior to the posterior edge of the hypurals.

Daily age was estimated from counts of sagittal otolith microincrements, which were validated as daily by McBride.[2] Otoliths with a maximum length less than about

[1] Hales, L. S., Jr., R. S. McBride, E. A. Bender, R. L. Hoden, and K. W. Able. 1995. Characterization of non-target invertebrates and substrates from trawl collections during 1991–1992 at Beach Haven Ridge (LEO-15) and adjacent sites in Great Bay and on the inner continental shelf off New Jersey. Technical report (contribution 95-09), 34 p. Institute of Marine and Coastal Sciences, Rutgers, The State University of New Jersey, New Brunswick, NJ.

[2] McBride, R. S. In review. Spawning, growth, and overwintering size of searobins (Triglidae: *Prionotus carolinus* and *P. evolans*).

500 µm were removed and mounted whole on glass slides in immersion oil. Otoliths longer than about 500 µm were mounted in nail polish on a glass slide, sanded with 1500 grit sandpaper along the sagittal plane, and polished with 0.3-µm grinding powder. Immersion oil was used liberally to enhance the clarity of all otoliths, and polarized light aided the viewing of microincrement structure. Microincrement counts were made with a compound microscope, typically at 400×. Slides were coded and microincrements were counted by one reader on three separate occasions. A constant of 4 days, representing the period between hatching and deposition of the first ring, was added to the mean microincrement count to estimate age since hatching (McBride[2]). Preserved (95% ETOH) *P. carolinus* and *P. evolans* were selected in a stratified (0.5-mm intervals), random manner to compare ages and lengths. Microincrement counts from this comparative material ranged, based on all individuals, between 0% and 32% of the mean microincrement count for each otolith (mean=12.0%; n=41).

Prionotus carolinus were collected in far greater numbers than *P. evolans* and they were examined in greater detail. Size and age distributions were initially defined from collections made during the period of peak seasonal abundance (i.e. late September 1991), when a random sample of 34 larvae was selected from a Tucker trawl sample for 23 September. Another sample of juvenile *P. carolinus* was selected from a 2-m beam trawl tow on 23 September 1991 at a station near the above plankton tow (Table 2). Four final samples were selected from 2-m beam trawl tows set one month later (21–22 October) at four stations along a transect of varying depths. Otoliths from all juveniles collected at these stations were analyzed (i.e. only fish that were mutilated or that had cracked otoliths or otoliths sectioned beyond the core were excluded). General methods of measuring and staging individual fish, and preparing otoliths, followed that described above. Sagittal microincrements were counted on two (for larvae) or three (for juveniles) separate dates by one reader. The range of these microincrement counts, for all individuals, was from 0.0% to 25.0% (mean=9.6%; n=127) of each mean count.

Results

Interspecific comparisons

Prionotus carolinus were more numerous and occurred more frequently than *P. evolans* in nearly all collections, typically by an order of magnitude (Table 1). Spawning by both species occurred from at least July to October offshore of southern New Jersey (Fig. 2). Modal size of larvae generally increased with time, but there were exceptions that indicated a pattern of multiple spawning events. For example in August 1991, modal size for *Prionotus* spp. and *P. carolinus* was notably smaller (3–4 mm) than the previous month (5–6 mm) (Fig. 3). Peak larval abundances varied somewhat between years but were highest from July to September.

Prionotus carolinus was the smaller but older congener at each developmental stage. Size and stage were com-

Table 1

Details of plankton and beam trawling data examined in our study. Larvae reported as *Prionotus* spp. were nearly all preflexion stages that did not exhibit diagnostic characters for separating these two congeners. For beam trawl collections, total number of fish are shown at left and the number of age-0 fish are shown to the right (in parentheses). See Figure 1 for general sampling areas.

Sampling area	Tow depth (m)	Net type	Year	Months	Number of cruises	Number of tows	Number of fish collected		
							P. carolinus	*P. evolans*	*Prionotus* spp.
Beach Haven Ridge (landward and seaward only)	0–15	1×1-m Tucker trawl (505-µm mesh)	1991	Jul – Dec	5	21	1274	48	84
			1992	Jan – Nov	14	56	17	0	17
	12–16	2-m beam trawl (6-mm mesh)	1991	Jul – Dec	6	61	459 (403)	40 (32)	0
			1992	Jan – Nov	14	89	122 (79)	26 (18)	0
Other ridge stations	6.1–17	2-m beam trawl (6-mm mesh)	1991	Aug – Oct	4	22	286 (284)	11 (8)	0
			1992	Jan – Nov	13	46	38 (35)	2 (1)	0
Ridge-transect stations	17–24	2-m beam trawl (6-mm mesh)	1991	Oct	1	7	73 (73)	0	0
			1992	Apr – Nov	4	28	114 (111)	0	0
Great Bay	1.4–8	2-m beam trawl (6-mm mesh)	1992	Aug – Oct	3	38	0	1 (1)	0

Table 2

Daily age, size, and hatching dates for planktonic (flexion and postflexion stages) larvae and benthic (settled stage) juveniles of *P. carolinus* collected in September and October 1991, offshore of southern New Jersey (see Fig. 8 for station locations). Data are presented as means (±1 standard error), and the range of values is given in parentheses. Larvae were collected with a 1×1-m Tucker trawl (0.505-mm mesh) and juveniles with a 2-m beam trawl (6-mm mesh).

Date	Stage	Station	*n*	Age (days)	Length (mm)	Hatching date
23 Sep	flexion	OT5	9	15.4 ±0.73 (12–17.5)	5.3 ±0.20 (4.1–6.2)	8 Sep ±0.73 (6 Sep–11 Sep)
23 Sep	postflexion	OT5	25	17.7 ±0.53 (12–23.0)	7.0 ±0.20 (5.7–9.5)	5 Sep ±0.53 (31 Aug–11 Sep)
23 Sep	settled	OT5	23	37.4 ±1.91 24–61.3)	12.2 ±0.44 (8.5–15.8)	17 Aug ±1.91 (24 Jul–30 Aug)
21 Oct	settled	OT2	15	60.9 ±3.06 (46–94.7)	17.5 ±1.42 (12.8–30.4)	19 Aug ±3.06 (18 Jul–5 Sep)
21 Oct	settled	OT5	13	62.2 ±2.81 (52–90.7)	16.8 ±1.58 (12.8–35.3)	20 Aug ±2.81 (22 Jul–30 Aug)
22 Oct	settled	Sta. C	29	75.1 ±2.71 (54–134.0)	21.9 ±1.44 (13.1–59.4)	8 Aug ±2.71 (10 Jun–29 Aug)
22 Oct	settled	Sta. E	13	90.0 ±3.20 (69.3–105.3)	26.3 ±0.96 (20.2–33.7)	24 Jul ±3.20 (8 Jul–13 Aug)

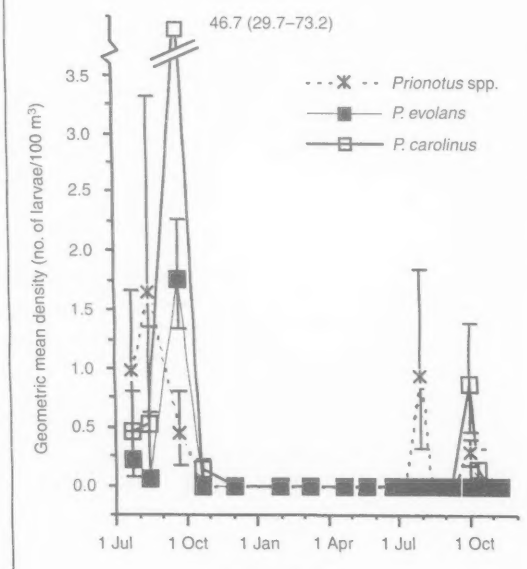

Figure 2

Density (geometric mean number of larvae per 100 m^3 [±1 standard error, SE]) of *Prionotus* spp., *P. carolinus*, and *P. evolans* larvae for each cruise near Beach Haven Ridge, based on daylight tows of a Tucker trawl at the landward and seaward stations (see Fig. 1). Note break in scale (range of SE bars are given in parentheses).

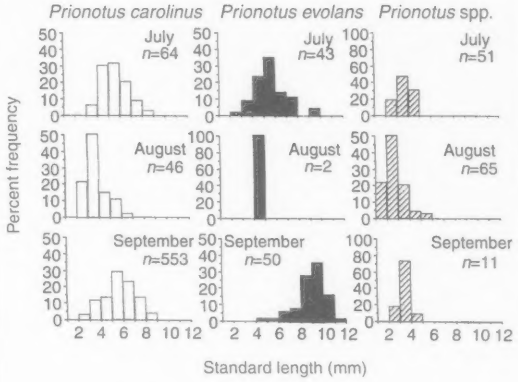

Figure 3

Size frequency of *Prionotus carolinus*, *P. evolans*, and *Prionotus* spp. from Tucker trawl collections near Beach Haven Ridge during July–September 1991. *n* = total number of larvae collected.

pared for 534 *P. carolinus* and 81 *P. evolans* collected with the Tucker trawl during both day and night. Flexion was complete at a larger size for *P. evolans* than for *P. carolinus* (range: 6.7–7.5 mm versus 5.4–6.8 mm SL), and planktonic postflexion *P. evolans* larvae were captured at larger sizes than postflexion *P. carolinus* (range: 6.7–11.9 versus 5.4–9.8 mm SL). *Prionotus evolans* completed flexion at a younger age than *P. carolinus* (approximately 13

versus 18 days after hatching) (Fig. 4). Both species settled as early as 18–19 days after hatching, but this was more characteristic of *P. evolans*; most *P. carolinus* did not settle until 24–25 days old.

Both species grew relatively slowly, and approximately linearly, during the larval and early juvenile period (i.e. ≤0.3 mm/d; Fig. 4, and next subsection). These slow growth rates, combined with the late peak in spawning (i.e. around August), resulted in small body sizes by the onset of winter. These smaller body sizes were particularly true for *P. carolinus*, for which the most pronounced size mode was 10–15 mm SL in autumn 1991 and 1992 (Fig. 5). At this time (i.e. September–December), individuals <50 mm SL constituted 85% of *P. carolinus* and 52% of *P. evolans* from all beam trawl tows combined; during autumn a majority of *Prionotus* spp. were <25 mm SL.

At beam trawl stations, densities of *P. carolinus* were consistently higher than those for *P. evolans* in both 1991 and 1992 (Fig. 6). Geometric mean densities of age-0 *P. carolinus* during the peak period of settlement (September–October) were much higher in 1991 (8.98 fish 100/m^2) than in 1992 (1.56 fish 100/m^2). Geometric mean densities of age-0 *P. evolans* during September–October were also higher in 1991 (0.32 fish 100/m^2) than in 1992 (0.09 fish 100/m^2). These interannual differences were consistent with higher larval densities of both species in 1991 versus 1992 (Fig. 2). Maximum densities of age-0 searobins at a single station reached 28.9 *P. carolinus* 100/m^2 and 3.2 *P. evolans* 100/m^2, both in September 1991. Searobins larger than 150 mm SL were collected infrequently from June to October; occasionally they were found together with age-0 conspecifics in the same beam trawl tows. Age-0 searobins of both species were collected primarily in continental shelf versus estuarine habitats during July–December (Fig. 7).

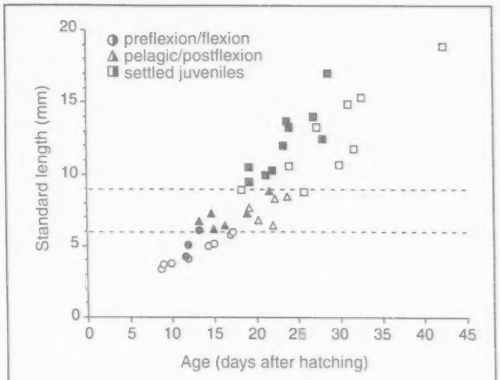

Figure 4

Relationship between daily age and length for *Prionotus carolinus* (open symbols) and *P. evolans* (filled symbols) for preflexion and flexion stages collected with a Tucker trawl (circles), postflexion stages collected with a Tucker trawl (triangles), and settled juveniles collected with a beam trawl (squares). The upper dashed line indicates the approximate size at settlement, and the lower dashed line indicates size at completion of flexion for both species.

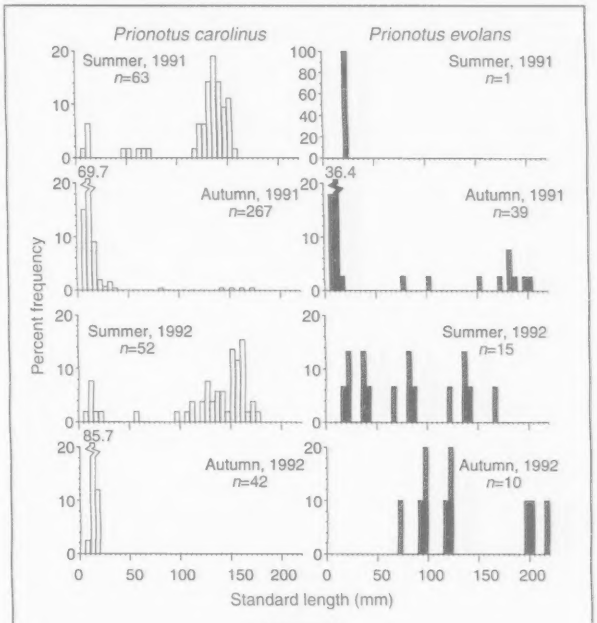

Figure 5

Size frequency of *Prionotus carolinus* and *P. evolans* for beam trawl collections near Beach Haven Ridge (daylight tows at the landward and seaward stations [Fig. 1]). Data were pooled by season: summer (May–August) and autumn (September–December). *n* = total number of fish collected. No data for January–April 1992 are shown because only a single fish (*P. carolinus*; 45 mm SL) was collected at these stations during this period.

Settlement of *Prionotus carolinus*

The seasonality of settlement by *P. carolinus*, although lasting from at least July to October, 1991, was punctuated by a 2–3 week period in September when the vast majority of larvae appeared to settle near Beach Haven Ridge (Fig. 8). Densities of age-0 *P. carolinus* near Beach Haven Ridge were very low during both July and August (geometric means ranging from 0.0 to 1.1 fish 100/m^2). During September, densities increased dramatically (range: 0.8–7.3 and 0.8–28.9 fish 100/m^2 on September 12 and 23–24, respectively). Individuals were collected at all stations along a depth transect, from 6 to 16 m, in late September. Settled, age-0 *P. carolinus* were still widespread and abundant in late October (0.0–13.3 fish 100/m^2), but they were not collected on 2 December 1991, and on 28 January and 10 March 1992.

Collections for 23 September 1991 demonstrate a wide range of *P. carolinus* developmental stages and ages present at Beach Haven Ridge (Fig. 9A). All flexion stages were present (6.5% preflexion, 26.0% flexion, and 67.4% postflexion; n=169). Planktonic larvae subsampled randomly from a Tucker trawl tow (n=34; Table 2) had hatched during a two-week period from

August 31 to September 11. Individuals collected by beam trawl on the same day (23 September 1991) had hatched about 2 weeks earlier (from 24 July to 30 August) than the above larvae (Fig. 9). These juveniles appeared to settle as young as 24 days after hatching and at sizes as small as 8.5 mm SL (Table 2). The total hatching date distribution for both larvae and newly settled juveniles collected on September 23 reflected a spawning period that ranged from late July to early September and that peaked in late August and early September.

Settled juveniles with a similar hatching date distribution were identifiable one month later at stations near Beach Haven Ridge, but not at stations farther offshore (Fig. 9, B and C). Fish collected near Beach Haven Ridge on 21 October 1991 had a hatching date distribution with a mode from late August through early September and the overall distribution was skewed to the left. This period was similar to the hatching date distributions for larvae and newly settled fish collected on 23 September 1991. In contrast, fish collected from offshore stations (i.e. stations C and E) on 22 October 1991 were 2–4 weeks older and 5–10 mm larger on average (Table 2, Fig. 9).

Plots of *P. carolinus* size versus age did not indicate any abrupt change at settlement, specifically for postflexion larvae and settled juveniles collected on 23 September 1991 (Fig. 10). Growth rates for this September collection fitted a linear model (SL=3.24+0.229[*age*]; r^2=0.77). Because *Prionotus* larvae hatch at about 3 mm SL (Yuschak, 1985), this model's y-intercept is biologically realistic. Growth rates of fish collected in October did not differ significantly between stations (ANCOVA: $prob._{slopes}$=0.13, $prob._{intercept}$=0.51); therefore the data were pooled. Linear, least squares regression of all data produced an unrealistic y-intercept (SL=–7.01+0.382[*age*]; SE_a=2.0; r^2=0.74). This model was rerun after restricting the y-intercept to 3 mm and the resulting equation indicated that age-0 *P. carolinus* continued to grow at about 1 mm every 4 days (SL=3 +0.251[*age*]; r^2=0.65) as they had during the larval and settlement period.

Size and age of *P. carolinus* juveniles varied significantly along a 12-km transect (12–20 m depths; Fig. 1). The linear relationship: $Hatching\ age = 17.8 + 3.43 \times depth$; r^2=0.35, P<0.01; n=69) showed that for every two meters change in depth offshore the fish collected were about one week older on average (Fig. 11). Sampling in both 1991 and 1992 showed a consistent trend for larger (and presumably older) fish to be collected in deeper water in October and November (Fig. 12). After accounting for the effects of depth, or possibly the distance from shore, it appeared that fish reached a larger size in October of 1991 than in 1992 or that larger fish in 1992 were not found in the sampling area.

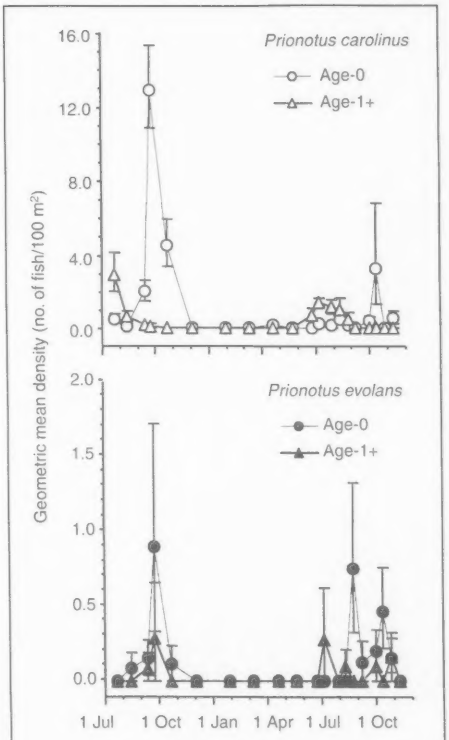

Figure 6

Density (geometric mean number of fish per 100 m² [±1 standard error]) of different cohorts of postsettlement *Prionotus carolinus* and *P. evolans* during daylight tows at the landward and seaward stations near Beach Haven Ridge. Note scale differences for each species.

Discussion

Spawning grounds and seasonality of spawning

Prionotus carolinus are more abundant than *P. evolans* in continental shelf habitats whether they are measured as eggs, larvae, juveniles, or adults (Keirans et al., 1986; McBride and Able, 1994; Able and Fahay, 1998; McBride et al., 1998; our present study). The low numbers of *P. evolans* observed in our study may be biased somewhat by our focused effort to sample the continental shelf rather than estuaries. *Prionotus evolans* reside in shallower, warmer habitats than do *P. carolinus* during the spawning season (McBride and Able, 1994). If *P. evolans* spawn to some degree in shallower waters or estuarine habitats, then this would at least partly explain the generally low abundance of *P. evolans* early life stages in our collections.

In general, we expect that larval distributions are good predictors of spawning locations for both *Prionotus* species because of the short (i.e. about three weeks) larval dispersal periods of these species (e.g. Houde and Zastrow [1993] reported several shelf species with planktonic duration >100 days). In some coastal areas, the distribution of *Prionotus* spp. eggs and larvae indicates that spawning may be limited to estuaries; however, the abundance of *Prionotus* larvae offshore of New Jersey suggests that spawning by these species occurs outside estuaries as well. For example, Merriman and Sclar (1952) did not find *Prionotus*

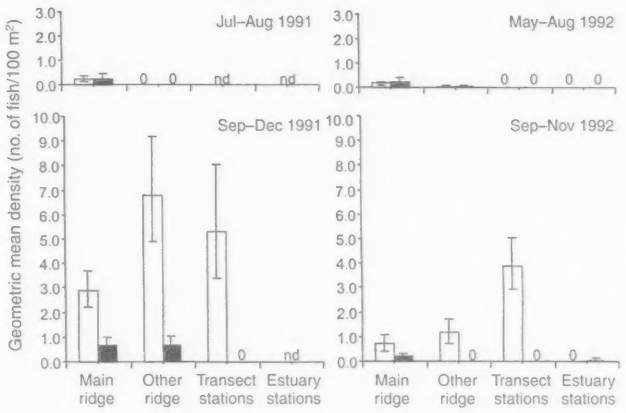

Figure 7

Density (geometric mean number of fish per 100 m^2 [±1 standard error]) of age-0 *Prionotus carolinus* (open bars) and age-0 *P. evolans* (filled bars) collected with a beam trawl from four major station groups (nd= no data; 0=sampling occurred but no *Prionotus* were collected). See Figure 1 and Table 1 for station groupings and locations.

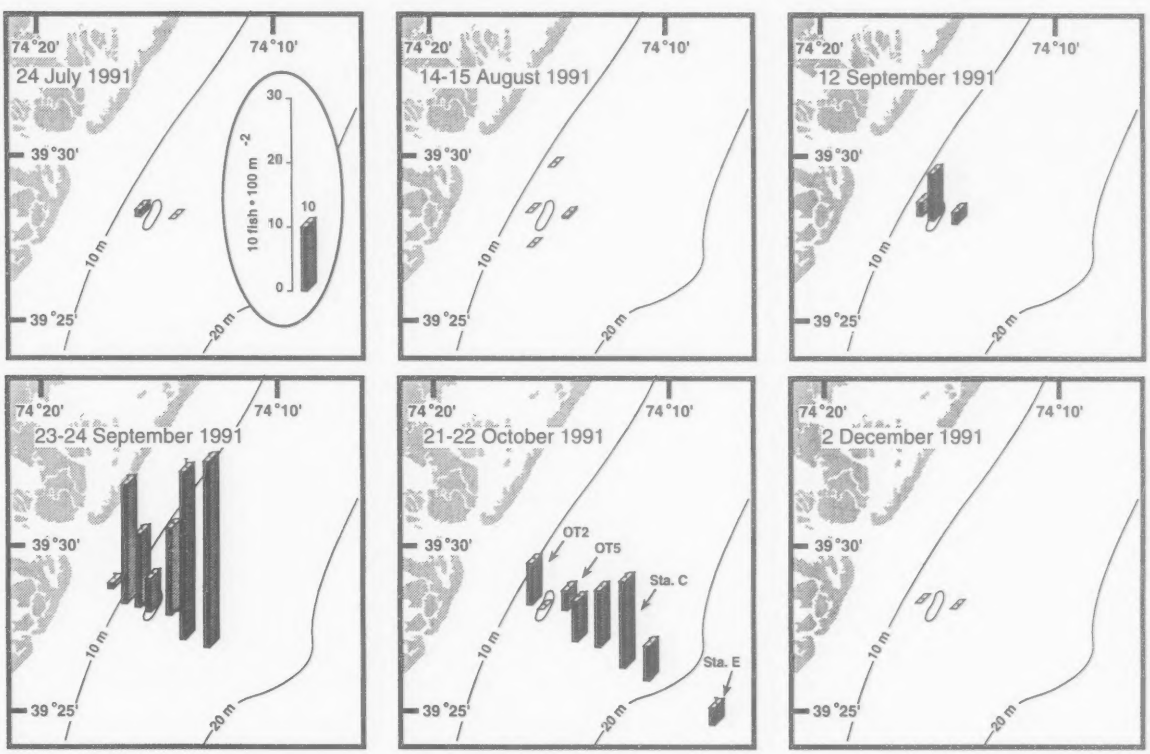

Figure 8

Densities (geometric mean [±1 standard error]) of age-0 *Prionotus carolinus* collected with a beam trawl during six consecutive cruises (July–December 1991). Number of stations varied between cruises. The scale bar indicates 10 fish/100 m^2.

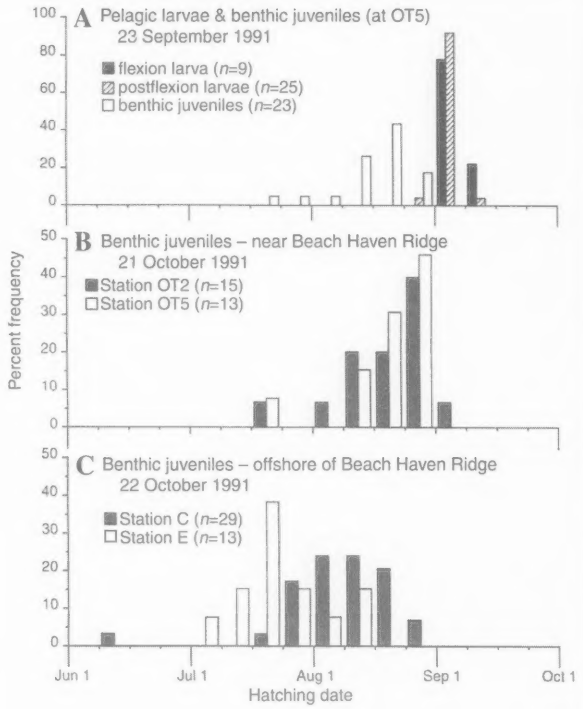

Figure 9

Hatching-date distributions for larval and newly settled juvenile *Prionotus carolinus* collected 23 September 1991 (**A**) and for juveniles collected on 21 October 1991 (**B**) and 22 October 1991 (**C**). See Figures 1 and 8 for locations of sampling stations.

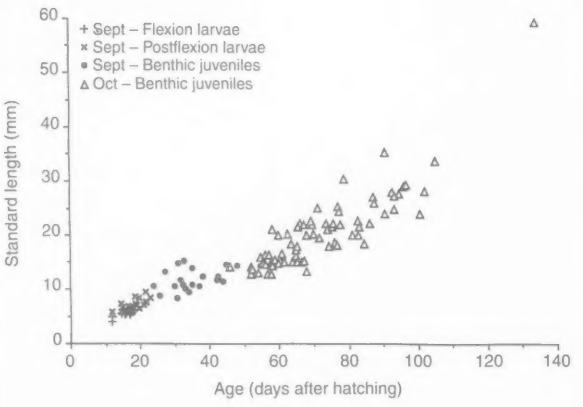

Figure 10

Age (days after hatching) and standard length (mm) for flexion, postflexion, and juvenile *Prionotus carolinus* collected seaward of Beach Haven Ridge on 23 September 1991 and 21–22 October 1991.

spp. eggs or larvae in Block Island Sound, and Able and Fahay (1998) did not observe *Prionotus* larvae above the continental shelf north or east of Hudson Canyon, New York. Instead there are many reports of *Prionotus* eggs, larvae, and juveniles in southern New England estuaries, specifically in Long Island Sound (Wheatland, 1956; Richards, 1959; Williams, 1968; Richards et al., 1979) and Narragansett Bay (Herman, 1963; Bourne and Govoni, 1988; Keller et al., 1999). Thus, the relative importance of estuaries versus shelf habitats as spawning grounds for *Prionotus* may vary in other regions compared with our results for New Jersey. Nonetheless, *Prionotus* spawning seasonality appears to follow a pattern similar to that of other species with a wide latitudinal range that have a shorter spawning season at higher latitudes (e.g. Conover, 1992) and that spawn later in the south (e.g. Barbieri et al., 1994). An important departure from this general trend is that *Prionotus* reproductive seasonality may vary not only with respect to latitude but along an estuary-shelf gradient as well. Because adults of both *Prionotus* species enter estuaries early in the spring and migrate back out to the shelf in summer (McBride and Able, 1994), we postulate that spawning occurs first in estuaries at a given latitude. In support of this hypothesis are the collective results from our study and other published reports. After the summer spawning peak within estuaries such as Chesapeake Bay and Long Island Sound, *Prionotus* spawn during August and September offshore of Chesapeake Bay and New Jersey. In contrast, spawning does not continue into late summer offshore of southern New England (Pearson, 1941; Richards et al., 1979; Able and Fahay, 1998).

To explain this potentially novel spawning pattern does not require any new controlling mechanism other than that used to explain spawning by other coastal fishes of the region. Temperature and photoperiod are known to influence spawning activity in fishes (Burger, 1939) and may influence spawning seasonality of searobins. Water temperatures offshore of the middle Atlantic seaboard are known to fluctuate widely both temporally and spatially (Colvocoresses and Musick, 1984) and this fluctuation affects the spawning pattern of many species. For example, a simple south to north progression of spawning activity above the shelf is evident for *Centropristis striata* (Able et al., 1995) and *Scophthalmus aquosus* (Morse and Able, 1995). For *Prionotus*, however, we propose that spawning seasonality is controlled by an interaction between latitudinal and estuarine gradients of temperature (i.e. earlier spawning in estuaries occurs because of earlier warming of these shallow embayments). Temperature has already been shown to affect the distribution of *Prionotus* adults along both latitudinal and estuarine gradients (McBride and Able, 1994;

McBride et al., 1998). Because few other species use both estuarine and shelf habitats for spawning, such patterns are not commonly observed.

Linking metamorphosis and settlement

Prionotus carolinus are often ranked as among the most abundant species in regional trawling surveys for adult fish or plankton surveys for larval fish (McBride and Able, 1994). The results from the small-mesh beam trawl used in our experiment demonstrate that the juvenile stages of *P. carolinus* are also very abundant offshore. Age-0 *Prionotus* spp. are found in estuaries, as discussed above for the southern New England region, but our observation of high densities of juvenile *Prionotus* in shelf habitats offshore of New Jersey suggest that neither species requires estuarine nursery habitats during their life cycle. Most searobins complete their life cycle in continental shelf habitats (Hoff, 1992), with the notable exception of *P. scitulus* whose young are concentrated in lower salinity, estuarine habitats (Ross, 1978).

Our findings of age and size at settlement largely agree with Yuschak and Lund's (1984) and Yuschak's (1985) descriptions of early development of cultured specimens. The developmental rate of cultured specimens of *P. carolinus* and *P. evolans*[3] did not differ notably from our observations of field-collected individuals, which further supports our conclusion that neither species delays settlement. *Prionotus evolans*, cultured at 20°C, were all at preflexion and flexion stages after 11–13 days; they were at flexion and newly postflexion stages after 18–20 days; and all were at the postflexion stage at 25 days. All available *P. carolinus* specimens, cultured at 15°C, were less than 20 days old; they followed a similar, if slightly slower, rate of development compared with *P. evolans*. Fin-ray development, which greatly facilitates locomotion, is complete in postflexion individuals. Prehensile, chemosensory pectoral rays, which would facilitate benthic feeding, are completely separated by 11.5 mm SL. Thus, on the basis of cultured and field-caught specimens, both species are well developed (i.e. are similar to adults) and well-suited for a bottom-feeding and swimming life style as they complete flexion. Other species delay metamorphosis to settle during favorable lunar phases (Sponaugle and Cowen, 1994), but settlement by *Prionotus* was so concentrated in a single month (i.e. September) that we could not test spawning or settlement cycles in more than one month. Nevertheless, because larvae of *Prionotus* species commonly bury themselves in loose substrate (Bardach and Case, 1965), and this material was common to all our sampling stations (Hales et al.[1]), competent larvae are likely not habitat limited (one mechanism identified with the delay of settlement).

The variation of *P. carolinus* sizes and ages along a depth gradient could be caused by one or a combination of three processes. There could be differential larval survivorship, juvenile movements, or adult reproduction rates

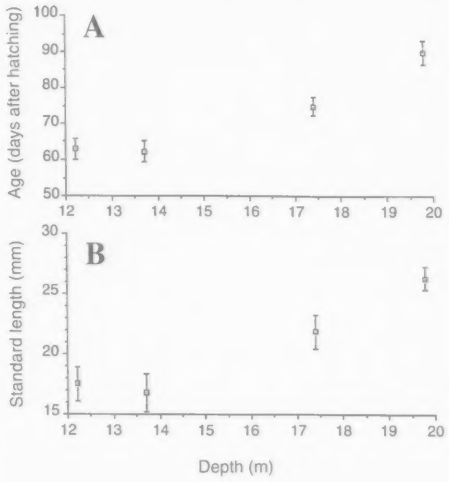

Figure 11

Age (**A**) and size (mean ±1 standard error) (**B**) of juvenile *Prionotus carolinus* plotted in relation to depth. Data are for fish collected on 21–22 October 1991 (near and offshore of Beach Haven Ridge: stations OT2, OT5, C, and E) and aged by using sagittal microincrements (see Table 2 and Fig. 9 for sample sizes).

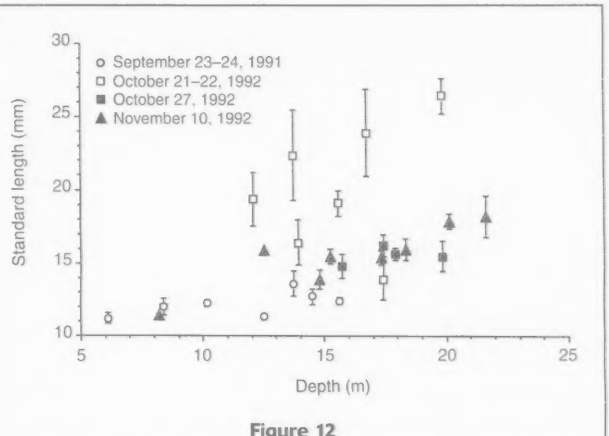

Figure 12

Standard length (mm; mean [±1 standard error]) of juvenile *Prionotus carolinus* in relation to depth for four separate cruises in 1991 (open symbols) and 1992 (filled symbols). All benthic juveniles collected were included in these calculations.

[3] This material was cultured by P. Yuschak (see Yuschak and Lund [1984] and Yuschak [1985]) and has been examined by R.S.M.

across the shelf to account for this spatial pattern of older and larger juveniles farther offshore. The last process was identified earlier as potentially important. Testing and eliminating these hypotheses, however, requires spatially explicit larval distribution data, in addition to the benthic data that we collected, which would allow a comparison of pre-and postsettlement distributions with abundance of *Prionotus* propagules. Spatially explicit environmental data would also be useful because we observed dynamic changes in the physical parameters in our sampling area, and we suspect that these could affect *Prionotus* survival. Vertical stratification of the water column was noted near Beach Haven Ridge on 14 August 1991, but not during cruises in September or October 1991. Low dissolved oxygen levels near the bottom of the ridge, at about 3 ppm (in contrast to >8 ppm in the upper water column) could have negatively affected settlement rates near the ridge in 1991. Stratification near the ridge was also noted in 1992 with similarly depressed levels of dissolved oxygen (Hales et al.[1]). Low dissolved oxygen offshore of New Jersey is not uncommon (Falkowski et al., 1980; Glenn et al., 1996) and may be another process that can contribute to geographic variations in size and age of *Prionotus* species offshore of the middle Atlantic states. We postulate that spatially explicit patterns of reproductive seasonality and age-0 fish size for *P. carolinus* and *P. evolans* within coastal waters offshore of the middle Atlantic states are related to each other because the short planktonic larval durations for both species limit larval dispersal. Interannual variations in water temperature or vertical stratification of oxygen concentrations may be proximate causes for these geographic variations of reproductive seasonality and age-0 size. These patterns could be somewhat unique to searobins, compared with other regional fishes, because searobins use both estuarine and shelf habitats for spawning.

Acknowledgments

R. Cowen, J. Hare, J. P. Grassle, R. Loveland, and C. L. Smith contributed thoughtful discussions and helpful comments on earlier drafts. S. Richards provided cultured specimens of searobins and miscellaneous data that had been used in P. Yuschak's research. This study was part of a doctoral dissertation (R. S. M.) and was supported by the Institute of Marine and Coastal Sciences (IMCS), Rutgers University Marine Field Station, Anne B. and James H. Leathem Fund, Manasquan Marlin and Tuna Club, NOAA National Undersea Research Program for the Middle Atlantic Bight, and NOAA Sea Grant Program. Final preparation and revision of this manuscript were made while the senior author was employed by the Florida Marine Research Institute. We thank all of the above.

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Abstract—In trawl surveys a cluster of fish are caught at each station, and fish caught together tend to have more similar characteristics, such as length, age, stomach contents etc., than those in the entire population. When this is the case, the effective sample size for estimates of the frequency distribution of a population characteristic can, therefore, be much smaller than the number of fish sampled during a survey. As examples, it is shown that the effective sample size for estimates of length-frequency distributions generated by trawl surveys conducted in the Barents Sea, off Namibia, and off South Africa is on average approximately one fish per tow. Thus many more fish than necessary are measured at each station (location). One way to increase the effective sample size for these surveys and, hence, increase the precision of the length-frequency estimates, is to reduce tow duration and use the time saved to collect samples at more stations.

Assessing the precision of frequency distributions estimated from trawl-survey samples

Michael Pennington
Institute of Marine Research
Department of Marine Resources
Nordnesgaten 33
N-5005 Bergen, Norway
E-mail address:michael@imr.no

Liza-Maré Burmeister
Ministry of Fisheries and Marine Resources of Namibia, NatMIRC
PO Box 912
Swakopmund, Namibia

Vidar Hjellvik
Institute of Marine Research
Department of Marine Resources
Nordnesgaten 33
N-5005 Bergen, Norway

Manuscript accepted 21 August 2001.
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Survey-based assessments often appear to provide a more accurate prognosis of the status of a fish stock than catch-based assessments (Nakken, 1998; Pennington and Strømme, 1998; Korsbrekke et al., 2001). An advantage that survey-based assessments have over those based on commercial catch statistics is that the uncertainties associated with survey estimates can be studied and quantified, and based on such research, survey methods, and ultimately stock assessments, can be improved (Godø, 1994). In contrast, it is generally difficult to determine either the accuracy or the precision of estimates based on commercial catch data, and it is not clear how to improve, at a reasonable cost, the collection of catch data so that these data would more accurately reflect the mortality caused by fishing (Christensen, 1996).

Trawl surveys provide estimates of the abundance or relative abundance of a fish stock and estimates of the relative frequency of various population characteristics, such as length, age, and stomach contents. In our study we examined the precision of survey-based estimates of the length-frequency distributions of cod and haddock in the Barents Sea, hake off South Africa, and hake off Namibia. The focus was on length, but the results are relevant for estimating the frequency distribution of other population characteristics.

Materials and methods

Survey length data

Bottom trawl survey length data for Northeast Artic cod (*Gadus mohua*) and Northeast Arctic haddock (*Melanogrammus aeglefinus*)[1] were collected during the Institute of Marine Research (Norway) winter and summer surveys in the Barents Sea. The surveys were stratified systematic surveys and at each station the trawl was towed for 30 minutes.[2]

[1] Also known as "Atlantic cod" and "haddock," respectively, according to *Common and scientific names of fishes from the United States and Canada*. 1991. Am. Fish. Soc. Spec. publ. 20, Besthesda, MD, 183 p.

[2] Aglen, A. 1999. Report on the demersal fish surveys in the Barents Sea and Svalbard area during summer/autumn 1996 and 1997. Unpubl. manuscr., Fisket og Havet NR. 7-1999. Institute of Marine Research, PO Box 1870 Nordnes, N-5817 Bergen, Norway.

The data for the Namibian deepwater hake (*Meluccius paradoxus*) were collected during bottom trawl surveys off Namibia conducted by the Ministry of Fisheries and Marine Resources of Namibia in conjunction with the Norwegian Agency for Foreign Aid (NORAD). For these surveys, tows of 30-minute duration were made at stations along transects perpendicular to the coast.[3]

The data for the deepwater hake for South Africa, were collected from during bottom trawl surveys off the west coast of South Africa. The surveys were conducted by the Marine and Coastal Management Centre, South Africa, by using a stratified random design. Tows of 30-minute duration were made at each station (see Payne et al., 1985).

Assessing the precision of length-frequency estimates

The sample of fish of a particular species measured during a survey is not a random sample of individual fish from the entire population but a sample of n clusters, one cluster from each station. Because fish caught together are usually more similar than those in the general population, a total of M fish collected in n clusters will contain less information about the population length distribution than M fish sampled randomly. One way to measure the information contained in a sample of length measurements is to estimate the number of fish that one would need to sample at random (the effective sample size) to obtain the same information on length contained in the cluster samples.

The effective sample size for cluster sampling can be defined and calculated as follows (Pennington and Vølstad, 1994; Folmer and Pennington, 2000). First estimate the population mean fish length and its variance based on the clusters of fish caught at n stations. Because both the lengths and the number of fish at a station are random variables, a ratio estimator is appropriate (Cochran, 1977). The ratio estimator, $\hat{R}$, of the mean length is given by

$$\hat{R} = \frac{\sum_{i=1}^{n} M_i \hat{\mu}_i}{\sum_{i=1}^{n} M_i}, \tag{1}$$

where M_i = the number of fish caught (either actual or estimated) at station i; and
$\hat{\mu}_i$ = an estimate of the average length of fish at station i.

For example, if the catch at a station is divided into strata and a random sample of fish are chosen in each stratum, then for that station $\hat{\mu}_i$ would be the stratified estimate of mean length. The estimated variance of $\hat{R}$ is approximately given by

$$\mathrm{var}(\hat{R}) = \sum_{i=1}^{n} \frac{(M_i / \overline{M})^2 (\hat{\mu}_i - \hat{R})^2}{n(n-1)}, \tag{2}$$

where $\overline{M} = \sum_{i=1}^{n} M_i / n$.

Next estimate the variance, σ_x^2, of the population length distribution. If m_i fish are randomly selected at each station (or if all fish are measured), then

$$\hat{\sigma}_x^2 = \frac{\sum_{i=1}^{n} \sum_{j=1}^{m_i} (M_i / m_i)(x_{i,j} - \hat{R})^2}{M - 1} \tag{3}$$

is an estimator of σ_x^2,

where $M = \sum_{i=1}^{n} M_i$ is the total number of fish caught during the survey; and
$x_{i,j}$ = the length of the j^{th} fish at station i.

For other sampling schemes at a station, first estimate the number of fish caught during the survey in each of L length bins, then (e.g. Bhattacharyya and Johnson, 1977)

$$\hat{\sigma}_x^2 = \frac{\sum_{k=1}^{L} f_k (y'_k - \hat{R})^2}{M - 1} \tag{4}$$

is an estimator of σ_x^2,

where f_k = the frequency of fish in the k^{th} length bin; and
y'_k = the bin's midpoint.

Now if it were possible to sample m fish at random from the population, then the variance of the sample mean would be equal to σ_x^2/m. The effective sample, m_{eff}, is defined as the number of fish that would need to be sampled at random so that the sample mean would have the same precision as an estimate based on a sample of n clusters. An estimate of the effective sample size for a particular cluster sample can be derived by substituting the estimates from Equation 2 and either Equation 3 or 4 into the equation

$$\frac{\hat{\sigma}_x^2}{\hat{m}_{eff}} = \mathrm{var}(\hat{R}). \tag{5}$$

The effective sample size is related to Kish's design effect (*deff*), which for estimating the mean from cluster sampling is defined by (Cochran, 1977)

$$deff = \frac{\mathrm{var}(\hat{R})}{\sigma_x^2 / m}$$

[3] Anonymous. 1999. Survey of fish resources of Namibia. Preliminary cruise report 1/99. NORAD-FAO/UNDP Project GLO92/013, 52. Unpubl. manuscr. NatMIRC, PO Box 912, Swakopmund, Namibia.

Table 1

Summary statistics for assessing the precision of the estimated length distributions of Northeast Arctic cod based on the winter and summer bottom trawl surveys in the Barents Sea. The estimated effective sample size is denoted by $\hat{m}_{eff}$, n is the number of stations at which cod were caught, M is the total number of cod caught, m is the number measured, $\bar{R}$ is the estimate of mean length, and var($\bar{R}$) is its variance.

Year	n	M	m	$\bar{R}$(cm)	var($\bar{R}$)	$\hat{m}_{eff}$	$\hat{m}_{eff}/n$	$(\hat{m}_{eff}/m) \times 100\%$
Winter								
1995	296	175006	47286	20.0	0.7	313	1.1	0.7
1996	314	209114	44021	18.0	0.3	511	1.6	1.1
1997	177	71418	25689	19.0	2.1	119	0.7	0.7
1998	197	60746	32536	22.1	0.7	394	2.0	1.2
1999	223	50192	21760	25.0	1.9	107	0.5	0.5
	Avg.	113295	34258			289	1.2	0.8
Summer								
1995	329	66643	46161	31.2	1.4	252	0.8	0.6
1996	341	115834	45286	24.4	0.6	478	1.4	1.1
1997	266	72093	26947	23.1	0.8	266	1.0	1.0
1998	218	72360	23461	25.1	1.1	184	0.8	0.8
1999	217	46593	23253	30.8	0.9	211	0.9	0.9
	Avg.	74705	33022			278	1.0	0.9

and, therefore, $m_{eff} = m/deff$. Some statistical software packages for the analysis of complex survey data, such as SUDAAN (Research Triangle Institute, 2001), generate estimates of the design effect.

Simulation techniques were used to examine the effect that reducing the total number of fish measured during a particular survey would have on the estimates of the mean length and the effective sample size. Length measurements consist of one or more subsamples from the fish caught at each station. The simulated estimates of the distributions of $\hat{m}_{eff}$ and $\bar{R}$ (given the actual fish measured during the survey) were generated by randomly selecting from every haul a maximum of k fish without replacement from each subsample. If fewer than k fish were in a subsample, then all were chosen. This was done 500 times for k = 10, 30, and 100, and each run produced values of $\hat{m}_{eff}$ and $\bar{R}$.

To assess the precision of an estimated length distribution, bootstrapping (Efron, 1982) was used to generate 95% confidence intervals for the proportion of fish in each 5-cm length bin. For each of 500 runs, n stations (the number of tows made during the survey) were randomly sampled with replacement and the confidence interval for each 5-cm length bin was based on the resulting 500 estimates of the proportion of fish in that bin. Finally, bootstrapping was used to examine how much the length of the 95% confidence intervals would increase if a maximum of 10 fish were selected from each subsample.

Results

Estimates of the effective sample size and associated statistics for survey-based estimates of the length composition of cod in the Barents Sea are presented in Table 1. The results indicate that for cod the estimated effective sample size is small compared with the number of fish measured. For example during the 1995 winter survey, 175,006 cod were caught, 47,286 were measured, and the effective sample size was 313 fish or 0.7% of the total number measured (Table 1). The average effective sample size for the winter surveys was 1.2 cod per tow and for the summer surveys, 1.0 cod per tow. The estimated effective sample sizes for the Northeast Arctic haddock survey data were, on average, approximately one fish per tow (Table 2).

The effective sample sizes for the survey estimates of the length distribution of deepwater hake off Namibia and off South Africa (Tables 3 and 4) followed the same pattern as for cod and haddock in the Barents Sea. In particular, the average effective sample size was 0.5 hake per tow for the Namibian surveys and 1.3 hake per tow for the South African surveys.

The simulated distributions of $\hat{m}_{eff}$ and $\bar{R}$, which demonstrate the effects of reducing the total number of measured fish on estimates of mean length, for the 1995 and 1999 winter surveys of cod in the Barents Sea are shown in Figures 1 and 2. For example, if a maximum of 30 fish were selected from each subsample at each station, then a total of 11,123 fish would have been measured during the 1995 survey compared with 47,286 fish that were actually measured. For 1995, $\bar{R}$ = 19.96 and the 95% confidence interval for $\bar{R}$ was (18.29, 21.63). As can be seen from Figure 1, all 500 simulated estimates of the mean based on the reduced sample size were well within the 95% confidence limits for $\bar{R}$. When the number of fish measured was reduced to a maximum of 10 fish per subsample for a total sample of 2597 fish, the simulated estimates were also

Table 2

Summary statistics for assessing the precision of the estimated length distributions of Northeast Arctic haddock generated by the winter and summer bottom trawl surveys in the Barents Sea. The notation is the same as that shown in Table 1.

Year	n	M	m	$\hat{R}$(cm)	var($\hat{R}$)	$\hat{m}_{\text{eff}}$	$\hat{m}_{\text{eff}}/n$	$(\hat{m}_{\text{eff}}/m) \times 100\%$
Winter								
1995	199	66009	22938	25.0	1.0	168	0.8	0.7
1996	235	54892	25525	32.0	2.9	69	0.3	0.3
1997	140	37441	13273	22.0	0.8	185	0.8	1.4
1998	144	12704	9620	23.9	1.0	169	1.2	1.8
1999	182	41612	12152	13.4	0.4	188	1.0	1.6
	Avg.	42532	16702			155	0.8	1.2
Summer								
1995	208	25771	15763	27.0	0.95	147	0.7	0.9
1996	163	14139	7338	31.1	3.65	51	0.3	0.7
1997	114	13560	4314	23.1	1.72	56	0.5	1.3
1998	89	7432	2699	21.3	0.34	170	1.9	6.3
1999	140	11922	5489	20.1	0.36	197	1.4	3.6
	Avg.	14565	7536			124	1.0	2.6

Table 3

Summary statistics for assessing the precision of the estimated length distribution of deepwater hake off Namibia based on bottom trawl surveys. The notation is the same as that shown in Table 1.

Year	n	M	m	$\hat{R}$(cm)	var($\hat{R}$)	$\hat{m}_{\text{eff}}$	$\hat{m}_{\text{eff}}/n$	$(\hat{m}_{\text{eff}}/m) \times 100\%$
Sep 1990	37	6671	1837	24.6	1.8	35	1.0	1.9
Jan 1991	19	3887	1329	29.2	3.3	19	1.0	1.4
Oct 1992	53	22369	5090	30.1	2.1	30	0.6	0.6
Apr 1992	63	33107	5411	34.0	2.8	30	0.5	0.6
Oct 1993	88	36814	8480	30.3	2.6	41	0.5	0.5
Jan 1993	70	36247	8208	37.3	2.9	33	0.5	0.4
Apr 1993	84	25746	7023	32.7	4.2	35	0.4	0.5
Jan 1994	60	30134	7997	28.4	10.0	13	0.2	0.2
Apr 1994	103	72012	17694	35.3	1.4	63	0.6	0.4
Oct 1994	105	70817	17216	28.1	1.9	44	0.4	0.3
Apr 1995	79	47585	14661	26.0	7.0	20	0.3	0.2
Jan 1996	105	57540	27834	30.3	2.9	45	0.4	0.2
Sep 1996	105	78562	24975	28.7	1.6	50	0.5	0.2
Jan 1997	122	54995	27648	28.5	4.6	29	0.2	0.1
Jan 1998	104	52573	15717	34.5	2.3	44	0.4	0.4
Jan 1999	104	68419	19305	28.4	4.1	30	0.3	0.2
	Avg.	43592	13152			35	0.5	0.5

well within the 95% confidence interval for $\hat{R}$ (Fig. 1). The results of the simulations for the winter survey in 1999 were similar to those for 1995 (Fig. 2).

Bootstrapped estimates of the 95% confidence intervals for the estimated proportion of fish in each 5-cm length bin for the 1995 and 1999 Barents Sea winter survey of cod are shown in Figure 3. The inner brackets denote the confidence interval based on the total number of fish actually measured and the outer brackets denote the confidence intervals if a maximum of 10 fish were measured per subsample.

Discussion and conclusions

For all the surveys examined, the effective sample size for the survey length data was much smaller than the total number of fish measured. The average effective sample size

Table 4

Summary statistics for assessing the precision of the estimated length distribution of deepwater hake off South Africa based on bottom trawl surveys. The notation is the same as that shown in Table 1.

Year	n	M	m	$\hat{R}$(cm)	var($\hat{R}$)	$\hat{m}_{\text{eff}}$	$\hat{m}_{eff}/n$	$(\hat{m}_{eff}/m)\times 100\%$
Jan 1985	75	75883	13863	29.3	0.7	70	0.9	0.5
Jul 1985	65	55704	10786	29.9	0.9	52	0.8	0.5
Jan 1986	86	82720	16216	28.2	0.3	132	1.5	0.8
Jan 1987	91	140685	18317	26.7	0.3	122	1.3	0.7
Jul 1987	76	80476	14774	27.0	0.8	68	0.9	0.5
Feb 1988	88	91828	17187	24.3	0.5	98	1.1	0.6
Feb 1989	33	234796	10115	25.7	0.1	207	6.3	2.0
Jan 1990	75	150814	23093	26.0	1.6	43	0.6	0.2
Jan 1991	73	226234	17115	27.2	0.9	38	0.5	0.2
Feb 1992	83	174364	24334	25.2	0.8	58	0.7	0.2
Jan 1993	81	102395	24922	26.0	0.6	89	1.1	0.4
Jan 1994	63	139268	28621	27.1	0.7	68	1.1	0.2
Jan 1995	81	137225	37481	26.4	0.5	97	1.2	0.3
Jan 1996	77	167765	31538	25.2	1.1	46	0.6	0.1
Jan 1997	88	219218	33537	24.2	0.7	70	0.8	0.2
Jan 1998	76	251050	26328	25.9	0.3	116	1.5	0.4
Jan 1999	74	218438	26144	25.4	0.5	91	1.2	0.3
	Avg.	149933	22022			86	1.3	0.5

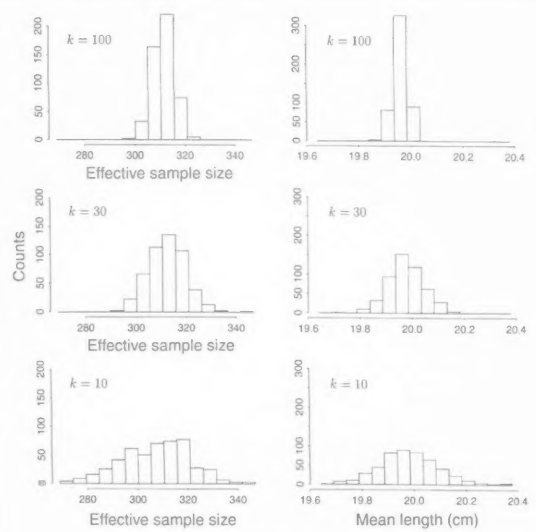

Figure 1

Simulated estimates of the distribution of the effective sample size, $\hat{m}_{eff}$, and of the mean length, $\hat{R}$, when the total number of fish measured is reduced for the 1995 winter survey in the Barents Sea. The top panel is when a maximum of k = 100 fish are selected per subsample for a total of m = 30,403 fish in each run; the middle panel, k = 30, m = 11,123; and the bottom panel, k = 10, m = 3911. The estimate of the population mean based on the entire sample (m=47,286) is 19.96 and its 95% confidence interval is (18.29, 21.63).

was approximately one fish per tow and it seems to be typical that the effective sample size for estimating length distributions is relatively small for trawl surveys. For example, the effective sample size for trawl surveys of haddock on Georges Bank was on average less than 0.5 fish per tow (Pennington and Vølstad, 1994) and for shrimp in a small area off West Greenland, about 3 shrimp per tow (Folmer and Pennington, 2000).

The reason that the effective sample sizes were small, and, therefore, the estimates of the length distributions were rather imprecise, given the number of fish that were measured, is that the lengths of fish in a haul tend to be more similar than those in the entire population. An additional factor is that the density of fish in a survey region is usually quite variable. To see this, consider the equation for the expected value of var($\hat{R}$). If every fish is measured during a survey, then subject to some assumptions, the expected variance of $\hat{R}$ when n stations are sampled is given approximately by (Pennington and Vølstad, 1994)

$$\text{var}(\hat{R}) = \frac{\sigma_x^2\left\{1+(\overline{M}-1+\sigma_m^2/\overline{M})\rho\right\}}{M},$$

where $\overline{M}$ = the expected mean catch per tow;
σ_m^2 = the tow-to-tow variance of catch;
$M(=n\overline{M})$ = the expected total number of fish caught;
σ_x^2 = the population variance of length; and
ρ = the coefficient of intrahaul correlation (see Cochran, 1977, p. 209) for length.

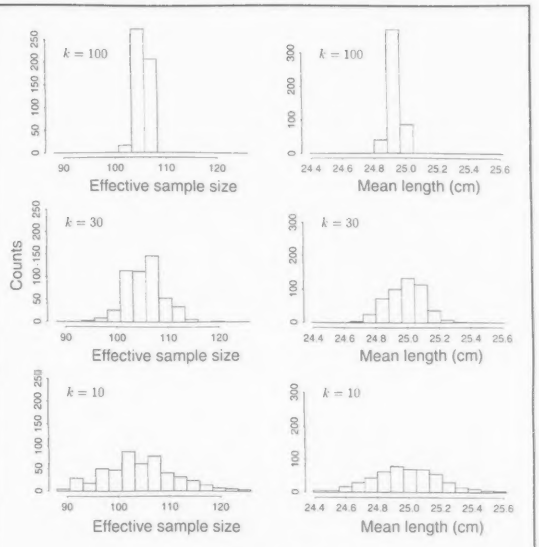

Figure 2

Simulated estimates of the distribution of the effective sample size, $\hat{m}_{eff}$, and of the mean length, $\hat{R}$, when the total number of fish measured is reduced for the 1999 winter survey in the Barents Sea. The top panel is when a maximum of k = 100 fish are selected per subsample for a total of m = 17,615 fish in each run; the middle panel, k = 30, m = 7240; and the bottom panel, k = 10, m = 2597. The estimate of the population mean based on the entire sample (m=21,769) is 24.96 and its 95% confidence interval is (22.26, 27.66).

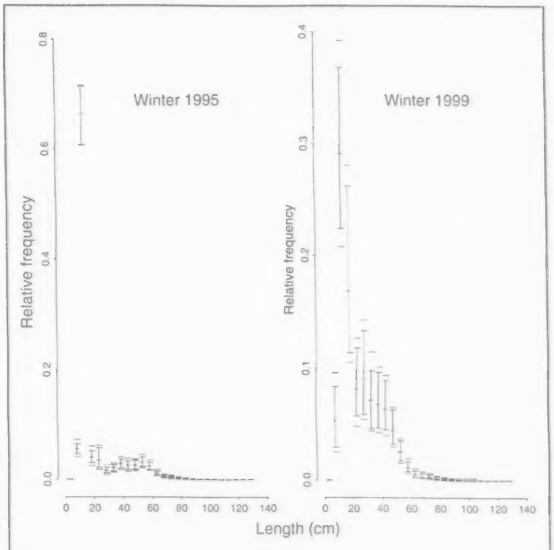

Figure 3

Bootstrapped estimates of the 95% confidence intervals for the proportion of cod in the Barents Sea in each 5-cm length bin, for winter 1995 and for winter 1999. The inner brackets denote the confidence intervals if the estimates are based on all the cod measured during the surveys and the outer brackets denote the confidence intervals if 10 fish are measured for each subsample.

If $\rho = 0$, then $\text{var}(\hat{R}) = \sigma_x^2 / M$ and the effective sample size is equal to M. However if $\rho > 0$ (i.e. fish of similar length tend to be caught together), then the terms in the parentheses can greatly increase the variance and thus drastically reduce the effective size. In particular, the term $\sigma_x^2 / \overline{M}$ is relatively large for trawl surveys. Finally, if $\rho < 0$, which is rarely if ever the case for trawl surveys, then the effective sample size will be larger than M.

The precision of estimates of other population characteristics, such as age distribution, can also be relatively low compared with the number of fish sampled if the particular attribute or measurement is more similar for fish caught together than for those in the general population. For example, the precision of estimates of mean stomach contents (Bogstad et al., 1995) or diet composition (Tirasin and Jørgensen, 1999) can be relatively low because of intrahaul correlation.

An effective sample size of one fish per tow does not mean only one fish should be measured at each station, but it implies that the only way to improve survey precision significantly is to increase the number of stations, i.e. to sample fish from as many locations as possible. The bootstrapped estimates of precision and the sampling simulations showed that reducing or increasing the number of fish measured (or caught and measured) at a station will not significantly affect the precision of length-distribution estimates. In general, if intracluster correlation is positive for an attribute, then it is usually best to take a small sample from as many locations as possible (e.g. Bogstad et al., 1995; McGarvey and Pennington, 2001).

It has been shown that tows of short duration are in general more efficient for estimating stock abundance than long tows (Godø et al., 1990; Pennington and Vølstad, 1991; Gunderson, 1993; Carlsson et al., 2000). Therefore one way to collect samples from more locations and improve overall survey efficiency without increasing survey cost is to reduce tow duration and use the time saved to increase the number of survey stations (Pennington and Vølstad, 1994). For example, if tow duration were reduced from 60 minutes to 15 minutes for a trawl survey of shrimp off West Greenland, then 44% more stations could be surveyed (Carlsson et al., 2000). Likewise, a reduction in tow duration from 30 minutes to 10 minutes for a trawl survey on Georges Bank would increase the number of survey stations by about 30% (Pennington and Vølstad, 1994).

The total number of fish caught would be fewer, on average, if tow duration was reduced, but estimates of fish density would be more precise and the resulting sample of individuals would be more representative of the entire population (Pennington and Vølstad, 1994).

Acknowledgments

We thank Rob Leslie (Marine and Coastal Management Centre, South Africa) for providing us with the South African survey data, and Jon HelgeVølstad (Versar, Inc., USA) and two anonymous referees for their constructive comments and suggestions.

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Estimated ages of red porgy (*Pagrus pagrus*) from fishery-dependent and fishery-independent data and a comparison of growth parameters

Jennifer C. Potts
Charles S. Manooch III

Center for Coastal Fisheries and Habitat Research
Beaufort Laboratory
National Marine Fisheries Service, NOAA
101 Pivers Island Road
Beaufort, North Carolina 28516-9722
E-mail address (for J. C. Potts): jennifer.potts@noaa.gov

Abstract–The red porgy, *Pagrus pagrus*, is an important reef fish in several offshore fisheries along the southeastern United States. We examined samples from North Carolina through southeast Florida from recreational (headboat) and commercial (hook and line) fisheries, as well as samples from a fishery-independent source. Red porgy attain a maximum age of at least 18 years and 733 mm total length. The weight-length relationship is represented by the ln-ln transformed equation: $W = 8.85 \times 10^{-6}(L)^{3.06}$, where W = whole weight in grams, and L = total length in mm. The von Bertalanffy growth equation fitted to the most recent, back-calculated lengths from all the samples is $L_t = 644(1 - e^{-0.15(t + 0.76)})$. Our study revealed a difference in mean length at age of red porgy from the three sources. Red porgy in fishery-independent collections were smaller at age than specimens examined from fishery-dependent sources. The difference in length-at-age may be related to gear selectivity and have important consequences in the assessment of fish stocks.

Manuscript accepted 20 August 2001.
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Red porgy, *Pagrus pagrus*, inhabit continental shelves in temperate and tropical waters throughout the Atlantic Ocean and Mediterranean Sea. The species supports fisheries in many countries and is heavily exploited. Since 1992, red porgy has ranked relatively high (38 of 200) in value among all finfish landed commercially in the southeastern United States.[1] Red porgy form a substantial part of overall reef fish landings, especially in North Carolina and South Carolina, although there is little directed fishing for the species. Commercial landings of red porgy from the southeastern U.S. peaked in 1982 at 535 metric tons (t) and declined to 134 t in 1993 (Potts and Burton[2]). Red porgy ranked second by weight for reef fish landed by recreational headboat[3] anglers through the early 1980s. Since then, headboat landings of red porgy have declined, and landings of vermilion snapper, *Rhomboplites aurorubens*, which are also declining, have now surpassed red porgy. White grunt, *Haemulon plumieri*, and gray triggerfish, *Balistes capriscus*, which were less preferred than other members of the snapper grouper complex, have increased in landings and now surpass red porgy.[4]

Mean weight of red porgy from the commercial and recreational fisheries has declined from 1.06 kg in the 1970s to 0.66 kg in 1997.[2] Minimum size regulations (305 mm total length) for recreational and commercial fisheries enacted in 1992 did little to increase mean weight in catches, although the headboat fishery did show a slight increase from 0.48 kg in 1991 and 1992 to 0.60 kg in 1997. Additionally, population biomass estimates for red porgy in the southeastern United States have plummeted from a peak of 3.27×10^6 kg in 1978 to 0.43×10^6 kg in 1992 (Huntsman et al.[5]). These trends suggest that red porgy stocks are being overexploited.

Age determination studies have been conducted throughout the range of red porgy. Manooch and Huntsman (1977) conducted the first comprehensive study using scales (n=1777) and whole otoliths (n=222) to age red porgy that were caught by recreational fishermen using hook-and-line gear off North Carolina and South Carolina when the species was lightly exploited (1972–74). Harris and McGovern (1997) aged red porgy from whole otoliths (n=4281) of

[1] General canvas. 1998. Unpubl. data. Miami Laboratory, National Marine Fisheries Service, 75 Virginia Beach Dr., Miami, Florida 33149.

[2] Potts, J. C., and M. L. Burton. 1999. Trends in catch data for fifteen species of reef fish landed along the southeastern United States. Unpubl. data. South Atlantic Fishery Management Council, 1 Southpark Circle, Charleston, SC 29407.

[3] A "headboat" is a fishing vessel that carries more than six passengers who pay per person (or by the "head") to go offshore fishing.

[4] Headboat annual summaries. 1998. Unpubl. data. Center for Coastal Fisheries and Habitat Research, Beaufort Laboratory, 101 Pivers Island Rd., Beaufort, NC 28516-9722.

[5] Huntsman, G. R., D. S. Vaughan, and J. C. Potts. 1994. Trends in population status of red porgy, *Pagrus pagrus*, in the Atlantic Ocean of North Carolina and South Carolina, USA, 1971–1992. Unpubl. data. South Atlantic Fishery Management Council, 1 Southpark Circle, Charleston, SC 29407.

fish caught from North Carolina to Florida with fishery-independent gear during 1979–81 and 1988–94. Nelson (1988) aged red porgy with scales (n=126) from fish caught in the northwestern Gulf of Mexico with fishery-independent hook-and-line gear and trap gear during 1980–82. In the eastern Gulf of Mexico, Hood and Johnson (2000) aged red porgy from sectioned otoliths (n=852) collected from headboat and commercial catches during 1995–96. Vassilopoulou and Papaconstantinou (1992) used scales from 138 red porgy that were taken with fishery-independent hook and line and trammel nets in the Mediterranean Sea during 1985–86, and Serafim and Krug (1995) aged red porgy from whole otoliths (n=358) that were collected by using commercial longlines and fishery-independent gear in the Azores during 1991–93. Researchers in the Canary Islands aged 1505 red porgy from commercial trap and longline samples during 1985–86 and 1991–93 (Pajuelo and Lorenzo, 1996), and researchers off the Argentinian coast used trawl-caught samples during 1972–81 to obtain 5859 red porgy that were aged from scales (Cotrina and Raimondo, 1997).

Predictions of fish populations from models rely heavily on input data sets, including age and growth. If samples used in the aging study are not representative of the entire population (i.e. the entire geographic range of the stock, full range of fish size, and different gear types), model predictions (e.g. spawning potential ratio [SPR]) can mislead management decisions. A comparative stock assessment of red porgy was done by using growth parameters and age-length keys generated from two studies: 1) fishery-independent data (Harris and McGovern, 1997) and 2) fishery-dependent data (Manooch and Huntsman, 1977; Potts et al.[6]). Each set of age and growth data was applied to fishery-dependent landings and length frequencies. The fishery-independent age and growth data produced a static SPR of 46%, which is well above the overfished definition (SPR<30%) as set forth by the South Atlantic Fishery Management Council (SAFMC). The fishery-dependent age and growth data produced a static SPR of 19% (Potts et al.[6]), which makes red porgy, by definition, overfished and which necessitates that stringent management measures be put in place to protect the stock.

The purpose of our study was to update the age and growth information on red porgy caught in the recreational and commercial fisheries operating along the southeastern United States. We present the von Bertalanffy growth model, weight-length relationship, and age-length keys for red porgy collected from the headboat hook-and-line fishery, commercial hook-and-line fishery, and fishery-independent samples. We also compare mean age at length of red porgy collected from recreational fisheries, commercial fisheries, and fishery-independent sources. We discuss how data source selection affects the growth parameters.

[6] Potts, J. C., M. L. Burton, and C. S. Manooch, III. 1998. Trends in catch data and estimated static SPR values for fifteen species of reef fish landed along the southeastern United States. Unpubl. data. South Atlantic Fishery Management Council, 1 Southpark Circle, Charleston, SC 29417.

Materials and methods

Sagittal otoliths were collected from red porgy landed by hook-and-line fishermen from the headboat (recreational) fishery (n=249) between 1989 and 1998 (59% from 1996 to 1998) and the commercial fishery (n=264) between 1997 and 1998 operating from North Carolina to southeast Florida. From the two fisheries, 64% of the samples came from North Carolina, 14% from South Carolina, and 22% from the east coast of Florida. Because of minimum size limit regulations (305 mm total length), the South Carolina Department of Natural Resources (SCDNR) Marine Monitoring and Prediction (MARMAP) Program supplied us with otoliths from red porgy that were smaller than those available from the fisheries (n=59) and an additional 62 samples ranging from 300 to 425 mm total length. These fish were caught primarily with Chevron traps off South Carolina during 1996 and 1997. Total length, whole weight, port of landing, and date of capture were recorded for each sample. The otoliths were stored dry in coin envelopes.

For age analysis, three transverse (dorsoventral) sections from the left otolith of each fish were taken by using a low-speed saw. One section was made on either side of the core, and the other encompassed the core. The sections were mounted on glass slides with thermal cement, and examined through a microscope at 80× and illuminated with reflected light. Clove oil was applied to each section to enhance the legibility of the growth zones on the section. The samples were put in sequential order from smallest to largest, and one reader counted the number of opaque zones in the otolith section. A second reader examined a random sample of the otoliths. If the readers disagreed on the age of a sample, they examined it again. If consensus was reached, the sample was retained; otherwise, the sample was discarded. Measurements from the core to the outer edge of each successive opaque zone and the otolith margin were taken along the lateral plane on the dorsal lobe of the section by using an ocular micrometer.

Analysis of the marginal increment (the distance between the last opaque zone and otolith margin) was used to validate the annual deposition of the opaque zones in the otoliths. For each age and month, the mean of the relative marginal increment, the ratio of the marginal increment to the distance between the last two opaque zones, was plotted. An opaque zone was considered an annulus if a minimum ratio was recorded for one month or season.

The relationship of fish length and otolith radius was described by regressing the observed total length on otolith radius (R_C). The linear equation was

$$L = a + b(R_C),$$

where L = total length in mm.

The back-calculated total lengths at each age were determined from the body proportional equation (Francis, 1990):

$$L_A = \left[(a + b\,R_A)/(a + b\,R_C)\right] L_C,$$

where L_A = back-calculated total length to annulus A;
a = intercept from the linear total length-otolith radius regression;
b = slope from the linear total length-otolith radius regression;
L_C = total length at time of capture;
R_A = otolith radius to annulus A; and
R_C = total otolith radius at time of capture.

The von Bertalanffy equation, $L_t = L_\infty[1 - \exp(-K(t-t_0)]$, was fitted to back-calculated lengths-at-ages for the most recently formed annuli (Ricker, 1975; Everhart et al., 1981; Vaughan and Burton, 1994). Growth parameters were estimated by using SAS PROC NLIN with the Marquardt Option (SAS Institute, 1982) for all aged fish and for fish obtained from fishery-dependent sampling.

Differences in mean back-calculated length at age for the most recently formed annulus for the three sample sources, i.e. recreational, commercial, and fishery-independent, were tested by using the general linear model analysis of variance.

To estimate the whole weight of gutted red porgy landed in the commercial fishery and to estimate stock biomass from assessment models, a regression of ln(*fish weight*) on ln(*fish length*) was performed and transformed to $W = a(L)^b$, where W = weight in g, and L = total length in mm.

Age-length keys were constructed from observed age at length by sample source in which the ages were unadjusted for time of year. Fish that were aged were assigned to 25-mm length intervals.

Results

Red porgy sampled for our study ranged from 176 to 733 mm TL and from 117 to 5895 g in whole weight. Ages were determined for 631 of 634 (99%) sectioned sagittal otoliths. Of those aged, 603 (95%) otoliths were considered legible to record measurements from the core to each successive opaque zone and the otolith margin. On twenty additional samples, we were able to measure only the otolith radius. Sectioned otoliths exhibited a recurrent pattern of alternating wide translucent zones and thin opaque zones. Estimated ages ranged from 1 to 18 years.

Analyses of marginal increment data indicated that the opaque zones were annular in nature and were formed in the spring (Fig. 1). Mean relative marginal increments for ages 2 through 8 were lowest in March through May and were the only months that had marginal increments equal to zero. They then steadily increased from June through October and remained high through February.

Back-calculated total lengths at age of red porgy were estimated from the parameters from the regression equation of total length (L) on otolith radius (R_c). The plot of length on radius was linear, and the linear regression equation that best fitted the data was $L = -132.84 + 10.87(R_c)$ (r^2=0.91, n=623). Using the Francis (1990) body proportional hypothesis, we found that weighted mean back-calculated lengths ranged from 103 mm for age-1 fish to 721 mm for age-18 fish (Table 1).

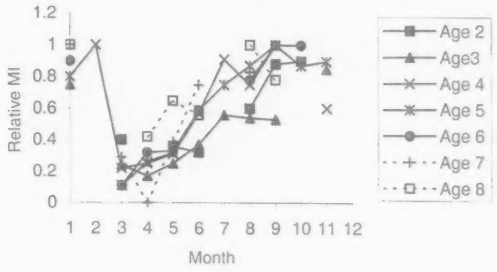

Figure 1

Mean monthly relative marginal increment (MI) of red porgy from the southeastern United States plotted by age.

The back-calculated lengths at the last annulus formation were used to estimate the von Bertalanffy equation. The equation parameters (±1 SE) were L_∞ = 644.72 ±17.93, K = 0.15 ±0.01, and t_0 = –0.76 ±0.10. The theoretical lengths at age ranged from 149 mm at age 1 to 605 mm at age 18. Theoretical lengths closely fitted the observed and back-calculated lengths through age 14 (Table 1). When we used fishery-dependent samples only to generate the von Bertalanffy growth equation, the resulting parameters (±1 SE) were L_∞ = 773.73 ±39.49, K = 0.09 ±0.01 and t_0 = –1.96 ±0.21. The fishery-dependent theoretical lengths at age ranged from 181 mm at age 1 to 646 mm at age 18.

We used ages 2 through 6 and data years 1996 through 1998 to compare length at age of the three data sources because the three sets overlapped for those ages and years. The ANOVA on the mean back-calculated length at age of the most recently formed annulus between sample sources indicated a significant difference in age at size between the MARMAP, headboat, and commercial red porgy samples (r^2=0.88; F-value=522.21; P=0.0001 for all combinations) and were represented by the model

$$TL = \alpha_0 + \gamma_C c + \gamma_h h + \sum_{j=1}^{5} \beta_j A_j,$$

where c = 1 if fishery = commercial, or c = 0 if fishery ≠ commercial;
h = 1 if fishery = headboat, or h = 0 if fishery ≠ headboat;
A_1 = 1 if age = 2, or A_1 = 0 if age ≠ 2, etc.; and
j = age categories.

Average TL = α_0 for fishery = fishery-independent and age = 6; average TL = α_0 + $\gamma_c c$ for fishery = commercial and age = 6; etc. The model indicated no year effect, and no interaction between fishery and age. MARMAP (fishery-independent) samples were smaller at age than those from the commercial and headboat fisheries. Although mean back-calculated lengths at age between headboat and commercial data sources were statistically different, the differences were slight (<15 mm) (Fig. 2).

Table 1

Mean back-calculated, mean observed, and theoretical total lengths (mm) of red porgy from the southeastern United States.

		Annulus number																	
Age (yr)	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	15	134																	
2	33	96	206																
3	136	98	208	274															
4	158	104	212	274	327														
5	136	105	212	274	326	363													
6	56	104	215	275	329	367	399												
7	31	107	216	284	342	381	413	441											
8	26	100	213	278	332	371	400	427	449										
9	6	106	221	283	337	377	410	438	461	483									
10	1	121	221	278	334	379	412	457	491	513	536								
11	2	112	215	275	329	362	395	427	449	476	498	520							
12	1	108	219	274	330	374	407	440	462	485	507	529	551						
14	1	111	226	294	351	385	419	442	465	487	510	533	556	567	579				
18	1	116	247	306	365	413	448	484	506	531	555	567	591	614	638	662	686	709	721
Total	603																		
Weighted mean TL		103	211	275	329	368	404	436	455	489	517	534	566	591	608	662	686	709	721
Incremental growth		103	108	64	54	39	36	32	19	34	28	17	32	25	17	54	24	24	12
Observed TL		198	236	303	350	386	423	459	470	508	547	536	562		590				733
Theoretical TL		149	218	278	329	374	410	443	471	495	516	534	549	562	574	583	592	599	605

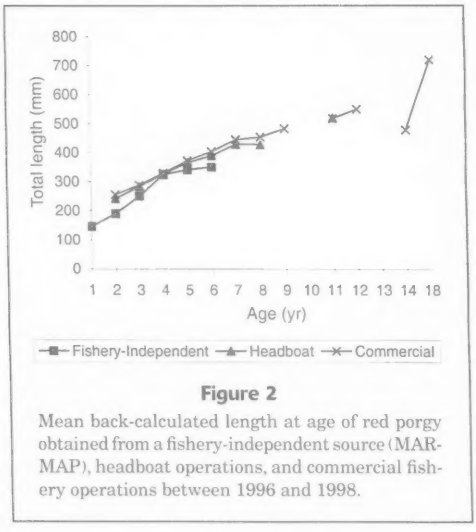

Figure 2

Mean back-calculated length at age of red porgy obtained from a fishery-independent source (MARMAP), headboat operations, and commercial fishery operations between 1996 and 1998.

The weight-length relationship for red porgy in the southeastern United States was best described by the converted ln-ln regression equation of $W = 8.85 \times 10^{-6}(L)^{3.06}$ (r^2=0.96, n=230, MSE=0.01).

Age-length keys by sample source are presented in Table 2. The fishery-independent key is appropriate for fishery-independent length data only. The headboat and commercial keys can be used to convert unaged length samples of red porgy from the fisheries operating in the southeastern United States to aged ones. Annual keys were not available owing to the small sample size from each year.

Discussion

In two previous aging studies on red porgy from the southeastern United States, populations were examined at two different levels of exploitation and different structures were used to determine age. Manooch and Huntsman (1977) sampled recreationally caught fish from an almost virgin stock off North Carolina and South Carolina during 1972–74. Although they used scales and whole otoliths, the main focus of their study and the analysis were on ages determined from scales. Of the 3278 scales analyzed, only 54% (1901) were legible enough to record ages. The main problem of aging red porgy with scales was the large number of regenerated scales.[7] Harris and McGovern (1997) used whole otoliths (n=4281) to age fish collected between 1979 and 1981 and between 1988 and 1994 from the MARMAP survey, a fishery-independent source. The 1988–94 samples in their study came from the area off North Carolina through northeast Florida, although 73% were collected in the area off Charleston, SC, between 32°N and 33°N. The samples were limited mainly to individuals below 450 mm TL (less than 1% of samples were

[7] Manooch, C. S. 1998. Personal commun. NOAA, Center for Coastal Fisheries and Habitat Research, 101 Pivers Island Road, Beaufort, NC 28516.

Table 2

Age-length keys for red porgy from the southeastern United States by sample source: fishery-independent, headboat, and commercial. Total length classes are in 25-mm intervals (i.e. 175 = 175–199).

		Age (yr)																
TL class	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Fishery-independent																			
175	11	10	1																
200	21	5	16																
225	7		1	6															
250	9			9															
275	10			10															
300	16			8	6	2													
325	20				11	9													
350	11				5	5	1												
375	14				6	8													
400	1					1													
425																			
450																			
475																			
500																			
525																			
550																			
575																			
725																			
Total	120																		
Headboat																			
175																			
200																			
225	3		3																
250	6		5	1															
275	28		5	23															
300	44			36	7	1													
325	48			15	31	2													
350	41			2	23	16													
375	37				11	21	5												
400	19					11	5	2	1										
425	11					2	5	2	2										
450	5						1	3	1										
475	2							2											
500	3							1		2									
525	2										1	1							
550																			
575																			
725																			
Total	249																		

continued

>450 mm). The data Harris and McGovern presented for the period between 1979 and 1981 showed that 8% of the samples for the reproductive study were greater than 450 mm TL. We sampled from a heavily exploited stock, and fish ranged up to 733 mm TL, and 14% of the fishery-dependent samples were greater than 450 mm TL. Additionally, our samples of red porgy were from a broader geographic range (52% from North Carolina, 30% from South Carolina, assuming all MARMAP samples were from South Carolina, and 18% from east coast Florida) than that of previous studies. Our distribution of samples more closely reflected the landings of red porgy in the southeastern United States. Also, we used sectioned otoliths, which have been determined to be the best struc-

Table 2 (continued)

		Age (yr)																
TL class	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Commercial																			
175																			
200																			
225																			
250																			
275	5		2	3															
300	25			22	3														
325	34			4	27	3													
350	28				24	4													
375	37				8	24	5												
400	44					29	14		1										
425	27					6	17	3	1										
450	31						7	16	8										
475	20							5	15										
500	7								1	6									
525	1											1							
550	1												1						
575	1														1				
725	1																	1	
Total	262																		

Table 3

Mean observed total length (mm) of red porgy from this study and others: 1 = our study (all data combined); 2 = Manooch and Huntsman (1977: scale data); 3 = Manooch and Huntsman (1977: otolith data); 4 = Harris and McGovern (1997: 1994 data year); 5 = Harris and McGovern (1997: 1988 data year).

	Study				
Age (yr)	1	2	3	4	5
1	198	238	229	218	224
2	236	290	288	294	297
3	303	342	331	306	329
4	350	382	374	328	379
5	386	419	402	344	445
6	423	451	425	362	399
7	459	483	453	386	431
8	470	505	474	374	406
9	508	527	496		448
10	547	543	534	449	
11	536	558	557		
12	562	604			
13		595			
14	590				
15		694			
16					
17					
18	733				

ture to age fish in many studies (Beamish, 1979; Boehlert, 1985; Smale and Punt, 1991).

Red porgy form their opaque zones during the spring along the southeastern United States. Both Manooch and Huntsman (1977) and Harris and McGovern (1997) reported that annulus formation occurred in red porgy during March and April. We found that the opaque zone formed from March through May. Springtime formation has also been reported from the Gulf of Mexico (Nelson, 1988; Hood and Johnson, 2000), from the Azores (May; Serafim and Krug, 1995) and from Argentinian waters (October; Cotrina and Raimondo, 1997). Pajuelo and Lorenzo, in their (1996) study of red porgy off the Canary Islands, found that the opaque zone was formed during the summer (June through October).

A comparison of the mean length at age from our study and that from Harris and McGovern's (1997) study from 1994 (Table 3) clearly reveals that red porgy caught with fishery-independent gear are much smaller at age for fish 3 years and older than fish caught with fishery-dependent gear. Mean size at age in our study was similar to data for fish 5 years and older reported by Manooch and Huntsman (1977) using otoliths, although our mean sizes were smaller that those reported for their scale data. Ages 1–5 of our study were a mix of MARMAP samples and fishery-dependent samples, which may explain why red porgy were smaller for those ages than those reported by Manooch and Huntsman (1977). The mean observed length at age from our study were on average 23 mm smaller than the corresponding lengths from Manooch and Huntsman (1977) for ages 6 through 12 as assigned by scales. The differences may

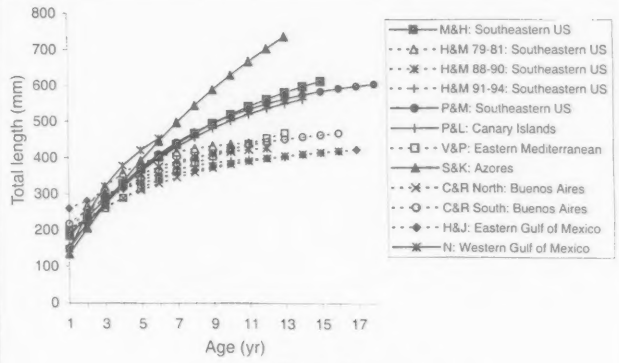

Figure 3

Comparison of von Bertalanffy growth curves from various locations in the Atlantic Ocean: M&H = Manooch and Huntsman (1977); H&M = Harris and McGovern (1997) from three separate data year sets; P&M = Potts and Manooch (this study); P&L = Pajuelo and Lorenzo (1996); V&P = Vassilopoulou and Papaconstantinou (1992); S&K = Serafim and Krug (1995); C&R = Cotrina and Raimondo (1997) from two study areas; H&J = Hood and Johnson (2000); N = Nelson (1988).

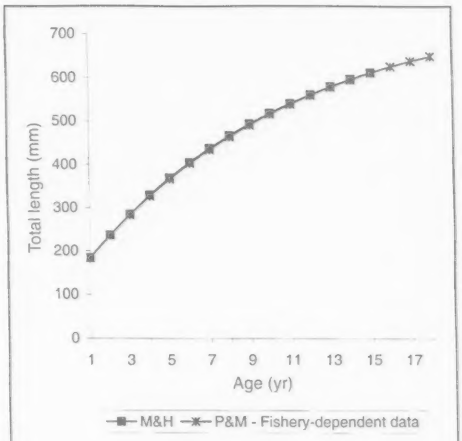

Figure 4

Comparison of the von Bertalanffy growth curve from Manooch and Huntsman (1977) using headboat data versus the resulting growth curves from headboat and commercial fisheries data from this study.

have been due to heavy fishing on the population, the small sample size of older age fish, or differences in assigned ages due to the structure used for aging, because the comparison of ages determined from otoliths was very close.

Harris and McGovern (1997) and Hood and Johnson (2000) have put forth the theory that heavy fishing pressure may cause a shift in the size and age structure of a population to smaller, slower growing fish. Our study does not support this theory. Cotrina and Raimondo (1997) demonstrated the differences in growth of red porgy caught from two areas off Argentina. Because we feel that our samples encompassed the full range of red porgy along the southeastern United States., our data more truly represents that population than the data from Harris and McGovern's (1997) study. We also feel that the perceived changes in length at age reported in Harris and McGovern's (1977) study may be confounded by the changes in sampling strategy of the MARMAP program between 1979 and 1994 (e.g. sampling gear used, locations of sampling, personnel, etc). Differences in growth of red porgy in the Gulf of Mexico between Hood and Johnson's (2000) study and Nelson's (1988) study may certainly be affected by the different locations the samples came from for the two studies. We suggest that further investigation into sample design and effects of habitat, temperature, fishing pressure, weather, fishing gear, etc. on fish populations is needed to help resolve differences between these studies.

The von Bertalanffy growth parameters L_∞ and K are integral components of stock assessment models. Samples for age determination should be representative of the target population (i.e. entire geographic range, all habitats, and all gear types used in the fisheries). Because back-calculated length-at-age information was unavailable to us from all previous studies, we compared the various von Bertalanffy growth curves with direct comparisons of length at age (Fig. 3). The growth curve of red porgy estimated by Manooch and Huntsman (1977), $L_t = 763(1 - e^{-0.096(t + 1.88)})$, is similar to our equation for all samples. Our calculated von Bertalanffy equation with fishery-dependent samples only was almost identical to that of Manooch and Huntsman (1977): $L_t = 774(1 - e^{-0.092(t + 1.96)})$ (Fig. 4). Although aging structures for the two studies were very different, ages were validated in both studies, and overall size ranges were similar.

In comparison with our study and that of Manooch and Huntsman (1977), the growth curves estimated by Harris and McGovern (1997) from their 1979–94 data had L_∞ values ranging from 411 to 451 mm TL. Red porgy in their study exhibited theoretical growth only from 58 to 69 mm, between ages 5 and 11. Red porgy from our study (all data combined) and Manooch and Huntsman's (1977) study theoretically grew from 164 mm to 172 mm, between ages 5 and 11. Also, the growth coefficients (0.27 to 0.34: 1979–94 data) from Harris and McGovern's (1997) data seemed high for red porgy in relation to those reported in other red porgy age and growth studies (Table 4) (Manooch and Huntsman, 1977; Vassilopoulou and Papaconstantinou, 1992; Serafim and Krug, 1995; Pajuelo and Lorenzo, 1996; Cotrina and Raimondo, 1997; Hood and Johnson, 2000).

Studies using fishery-independent sources for red porgy showed smaller L_∞ and higher K values than those from most studies where a combination of commercial, recreational, or fishery-independent samples were used (Table 4). The differences in growth curves are likely a result of smaller fish in the fishery-independent samples and a consequent truncated upper-length range. Although Hood and

Table 4

Comparison of nine age and growth studies of red porgy from the eastern and western Atlantic Ocean. (Rec.=recreational fishery; Comm.=commercial fishery; F-I=fishery-independent). NC = North Carolina; SC = South Carolina SEFL = southeast Florida; NEFL = northeast Florida. n = number of fish in sample.

Study	Location	Aging structure	Age range (yr)	Total length range (mm)	Sample source and n	L_∞ (TL, mm)	K	t_0
Manooch and Huntsman (1977)	Southeastern U.S. (NC–SC)	scales	1–15	238–694[1]	Rec. n=1777	763	0.10	–1.88
Our study	Southeastern U.S. (NC–SEFL)	sectioned otoliths	1–18	176–733	Comm., Rec., and F-I n=631	644	0.15	–0.76
Pajuelo and Lorenzo (1996)	Canary Islands	sectioned otoliths	0–14	97–572	Comm. and F-I n=1858	640	0.14	–0.99
Serafim and Krug (1995)	Azores	whole otoliths	1–13	204–722[1,2]	Comm. and F-I n=358	1172–1193[2]	0.06–0.07	–0.70 through –1.70
Hood and Johnson (2000)	Eastern Gulf of Mexico	sectioned otoliths	1–17	194–489	Comm. and Rec. n=854	459	0.11	–6.6
Harris and McGovern (1997) 1979–94 data	Southeastern U.S. (NC–NEFL)	whole otoliths	1–13	218–449[1,2]	F-I n=4281	411–451[2]	0.27–0.34	–0.60 through –1.11
Vassilopoulou and Papaconstantinou (1992)	Eastern Mediterranean Sea	scales	1–13	193–465[1,2]	F-I n=151	639[2]	0.08	–3.56
Cotrina and Raimondo (1997)	Buenos Aires, Argentina	scales	0–16	124–480	F-I n=5859	447–499	0.15–0.15	–2.96 through –2.81
Nelson (1988)	Western Gulf of Mexico	scales	2–6	302–482[2]	F-I n=126	554[2]	0.28	–0.06

[1] Mean total length; actual range of lengths in sample were not readily available.

[2] Fork lengths were converted to total lengths by using $TL = 7.111 + 1.134(FL)$ (MARMAP data, South Carolina Department of Natural Resources, Charleston, SC).

Johnson (2000) used fishery-dependent samples, the largest fish in that study was 489 mm TL, and their samples came from primarily one location. Selectivity of fishing gear may also explain differences in growth parameters. For example, hook-and-line gear may catch faster growing and more aggressive fish, whereas traps and trawls may catch slower growing fish and overall smaller fish. We recommend that in future age and growth studies of any fish species, samples represent the full range of fish sizes in a population, including fish caught by many different gear types, and are obtained from the entire geographic range of the stock. Where practical, landings should be stratified and sampled accordingly.

Acknowledgments

We would like to thank the port agents of the National Marine Fisheries Service and the South Carolina Department of Natural Resources MARMAP personnel for providing us with otolith samples. Jim Waters and Doug Vaughan, NOAA's Center for Coastal Fisheries and Habitat Research, were instrumental in the statistical analysis of the length-at-age data and provided thoughtful comments on the manuscript. Dean Ahrenholz and Joe Smith also of NOAA's Center for Coastal Fisheries and Habitat Research provided a critical review of the manuscript.

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Bycatch in the tuna purse-seine fisheries of the western Indian Ocean

Evgeny V. Romanov

Southern Scientific Research Institute of Marine Fisheries and Oceanography (YugNIRO)
2, Sverdlov St.
98300, Kerch, Crimea, Ukraine
E-mail address: island@crimea.com

Abstract—Bycatch taken by the tuna purse-seine fishery from the Indian Ocean pelagic ecosystem was estimated from data collected by scientific observers aboard Soviet purse seiners in the western Indian Ocean (WIO) during 1986–92. A total of 494 sets on free-swimming schools, whale-shark-associated schools, whale-associated schools, and log-associated schools were analyzed. More than 40 fish species and other marine animals were recorded. Among them only two species, yellowfin and skipjack tunas, were target species. Average levels of bycatch were 0.518 metric tons (t) per set, and 27.1 t per 1000 t of target species. The total annual purse-seine catch of yellowfin and skipjack tunas by principal fishing nations in the WIO during 1985–94 was 118,000–277,000 t. Nonrecorded annual bycatch for this period was estimated at 944–2270 t of pelagic oceanic sharks, 720–1877 t of rainbow runners, 705–1836 t of dolphinfishes, 507–1322 t of triggerfishes, 113–294 t of wahoo, 104–251 t of billfishes, 53–112 t of mobulas and mantas, 35–89 t of mackerel scad, 9–24 t of barracudas, and 67–174 t of other fishes. In addition, turtle bycatch and whale mortalities may have occurred. Because the bycatches were not recorded by some purse-seine vessels, it was not possible to assess the full impact of the fisheries on the pelagic ecosystem of the Indian Ocean. The first step to solving this problem is for the Indian Ocean Tuna Commission to establish a program in which scientific observers are placed on board tuna purse-seine and longline vessels fishing in the WIO.

Manuscript accepted 20 March 2001.
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One of the most important requirements of the UN Convention on the Law of the Sea of 1982, which determines strategies for exploitation of marine living resources (Article 119, b), is to take into account the impact of fisheries on ". . . species associated with or dependent upon harvested species with a view to maintaining or restoring populations of such associated or dependent species above levels at which their reproduction may become seriously threatened. . ." (United Nations, 1983). Estimating the magnitude of bycatch is one of the first steps to determine the impact of fisheries on associated species.

Tuna purse-seine fisheries probably apply the most intensive direct human impact on the tropical epipelagic ecosystems in all oceans. Because of the worldwide scale of purse-seine fisheries, an assessment of their impact on associated and dependent species is essential.

Two tunas, yellowfin *Thunnus albacares* (Bonnaterre, 1788) and skipjack *Katsuwonus pelamis* (Linnaeus, 1758), are the target species of most purse-seine fisheries. In this study bycatch is defined as the fraction of the catch that consists of nontarget species (including other species of tuna) that are encircled by the fishing gear and are unable to escape by themselves. Bycatch of associated and nonassociated species during purse-seine fishing for tropical tunas may be rather high, and generally depends on fishing tactics.

The species composition of bycatch in purse-seine fisheries depends on the structure, behavior, and spatial organization of surface multispecies aggregations. Schools of different tuna species and other pelagic fishes, marine mammals, and other marine animals have aggregated distributions. From our observations and in the opinion of other researchers (Au and Perryman, 1985; Au and Pitman, 1986; Au, 1991; Cort, 1992), marine birds are also an integral component of the majority of these multispecies groups.

The tunas, as a rule, prevail by biomass and abundance in such groups. Tuna schools are traditionally classified by the visually distinctive part of the group or by whether they associate with floating objects or marine mammals (Scott, 1969; Petit and Stretta, 1989). "Free-swimming schools" may include associations between different species of tuna. For each type of school, its various components occur in different ratios.

Some epipelagic species that occur in the purse-seine bycatches are not members of multispecies aggregations. They, instead, may comprise members of the flotsam community or are tuna forage. Several associated components, such as whales and birds, usually escape or avoid the nets and do not become bycatch. Therefore, the composition of the catch often does not represent the actual species composition of the multispecies associations.

Assessments of bycatches have been made for the eastern Pacific Ocean purse-seine tuna fishery (Joseph, 1994; Garcia and Hall, 1995; Hall, 1996, 1998; Anonymous, 1997, 1998, 1999), where the bycatch problem attracted attention because of dolphin mortality during sets on dolphin-associated tuna schools. The economic, political, and ecological implications of this problem produced wide international attention (Charat-Levy, 1991; Joseph, 1991, 1994; Hall, 1998). Bycatch estimates for the western Pacific purse-seine tuna fisheries have been published also (Bailey et al., 1996).

In the western Indian Ocean (WIO), tuna-dolphin associations are well known in coastal pelagic zones, e.g. Gulf of Aden (Demidov[1]) and Sri-Lanka (de Silva and Boniface[2]). They are often used in small-scale troll and pole-and-line fisheries for locating yellowfin tuna. In offshore regions of the WIO tuna-dolphin associations are rare, purse seining for them is not practiced, and there is no dolphin bycatch problem. Perhaps for this reason, the magnitude of bycatch in the WIO is unknown, except for recent information on species composition (Santana et al., 1998). Bycatches are not recorded for tuna seiners operating in the WIO, except bycatches of nontarget tuna species. This paper represents a first attempt to estimate catches of associated species by tuna purse seiners in the WIO, based on scarce information collected by scientific observers.

Materials and methods

Bycatch assessments were based on data collected by YugNIRO scientific observers aboard Soviet (since 1992—Russian) tuna purse seiners in the WIO, during 1987, and 1990–91. The vessels were the "Rodina" type.[3] In addition, observer data collected in the same area aboard sisterships by AtlantNIRO[4] and "Zaprybpromrazvedka"[5] during 1986–90 and data by TINRO[6] and TURNIF[7] during 1990 and 1992 were used. The fishing vessels all used purse seines of 1800 m in length, 250–280 m in depth, and 90–100 mm mesh size in the bunt.

The principal goal of the observer sampling program was an estimation of the species composition of catches in this fisheries, biological analysis of the principal species, and estimates of the length and weight compositions of these principal species in the catches. The observers were placed on board opportunistically (i.e. if a vessel had a free sleeping bed and if there was available funding), without a sampling scheme and without preference to any vessel type. Thus, the sampling could be considered as random. Two other types of Soviet fishing vessels, "Tibiya"[8] and "Kauri,"[9] which took part in the Indian Ocean fisheries during 1985–87 and since 1991 (under the Liberian flag), were not sampled. In this study coverage rate was estimated as percentage of sampled catch to total catch.

The observers recorded the results of each set. The type of school, according to Scott (1969) and Petit and Stretta (1989), of each set was recorded. I considered sets for which an observer recorded catch in any quantity as positive sets. The average bycatch level was estimated for all positive sets.

For the positive sets, species composition, total weights, and numbers of each species in the catch were recorded. In the vessels of the "Rodina" type, the retained catch was frozen and stored separately. The retained catch was weighed after freezing while being moved to the ship's holds. In nine cases, the weight of some of the catch was estimated by the ship masters because the holds were overloaded and some catch was stored in the freezers till landing. Therfore estimates of retained catch are presented in this study as frozen weights rather than wet weights. The bycatch was estimated as wet weight. Only bycatch taken on board was sampled. The sets when bycatch was not taken onboard but discarded alive (usually with negligible target species catch) and malfunction sets, which do not produce any catch, were not analyzed in this study. Large species, sharks and billfishes generally, were weighed and counted. The weights of specimens heavier than 200 kg (i.e. Mobulidae) were estimated. When the bycatch was more than 200–300 kg, species composition and weight were estimated by using representative samples.

Sometimes the observer recorded the bycatch in numbers. In these rare cases, the total weights of the fishes were estimated from the average weights of these species in previous catches.

The observers had free access to every fish in the catch. Nevertheless, some observers had difficulties identifying some billfishes, sharks, and Mobulidae species. Therefore, I pooled the records with doubtful species identification into these three groups for my analysis. These are marked by "?" in the tables.

The data were grouped and analyzed by free-swimming schools (including associations between schools of different species of tuna) and associated schools. The latter included whale-associated schools and log-associated schools (associated with floating objects).

Schools caught in the area of seamounts and shoals—at the peaks of the Equator Seamount and at Saya-de-Malha bank—were considered free-swimming schools. Some observers did not record the type of floating objects that were set on; therefore the sets on natural floating objects (50% to 90% of the log sets sampled) and on fish aggregation devices (FADs) (10–50%) were grouped. Several log sets were made in areas with surface evidence of water masses or current interactions (rips). A set that could not be clearly identified as to set type was made in such an area and was treated as a log set because of the species composition of the catch and the occurrence of small scattered debris in the rips.

[1] Demidov, V. F. 1998. Personal commun. Southern Scientific Research Institute of Marine Fisheries and Oceanography (YugNIRO), 2, Sverdlov St., 98300, Kerch, Crimea Ukraine.

[2] de Silva, J., and B. Boniface. 1991. The study of the handline fishery on the west coast of Sri Lanka with special reference to the use of dolphin for locating yellowfin tuna (*Thunnus albacares*). *In* Indo-Pacific Tuna Development and Management Programme (IPTP) Coll. Vol. Work. Doc TWS/90/18., Vol. 4, p. 314–324. Food and Agriculture Organization of the United Nations (FAO), Viale delle Terme di Caracalla, 00100, Rome, Italy.

[3] Length overall: 85 m; GRT (gross tonnage): 2634; carrying capacity: ~1600 m^3.

[4] AtlantNIRO—The Atlantic Scientific Research Institute of Marine Fisheries and Oceanography, 5 Dmitry Donskoi St., 236000 Kaliningrad, Russia.

[5] The Department of Searching and Scientific Research Fleet of the Western Basin "Zaprybpromrazvedka," 5[a] Dmitry Donskoi St., 236000 Kaliningrad, Russia.

[6] TINRO—The Pacific Scientific Research Institute of Marine Fisheries and Oceanography, 1 Shevchenko Alley, 690600 Vladivostok, Russia.

[7] TURNIF—The Pacific Department of Fish Searching and Scientific Research Fleet, 2 Pervogo Maya St., 690600 Vladivostok, Russia.

[8] Length overall: 55.5 m, GRT: 736, carrying capacity: ~361 m^3.

[9] Length overall: 79.8 m, GRT: 2100, carrying capacity: ~1200 m^3.

Table 1

Numbers of sets sampled by year. Positive sets are sets in which an observer registered catch in any quantity .

	1986	1987	1988	1989	1990	1991	1992	Total
Total number of sets	115	102	30	41	113	54	39	494
Number of positive sets	68	62	28	41	92	53	33	377
Percentage of sets with catch	59%	63%	93%	100%	81%	98%	85%	76%

Table 2

Numbers of sets sampled by season and type of school.

	Seasons				
Type of school	Winter	Spring	Summer	Autumn	Total/positive
Free-swimming	136	35	27	8	206/121
Whale-shark–associated	2	0	0	0	2/2
Whale-associated	23	21	1	0	45/37
Log-associated	46	50	80	65	241/217
Total	207	106	108	73	494/377

Because tuna purse-seine fishing in the WIO is clearly seasonal (monsoons governing fishing techniques and operations), the data were analyzed by season. I followed Romanov's (1982) seasonal divisions, in accordance with long-term average seasonal variations in the monsoon atmospheric circulation for the WIO. The winter season (northeastern monsoon) lasts from December to March, the spring intermonsoon period falls during April and May, the summer (southwestern monsoon) lasts from June to August, and the autumn intermonsoon period lasts from September through November. The wind regime determines the onset and duration of the hydrological seasons, which do not quite coincide with seasons of atmospheric circulation owing to a considerable time lag of the processes occurring in the ocean. However, the wind regime is instrumental in determining the tactics of purse seining for tuna; therefore I used seasonal strata based on atmospheric rather than on hydrological processes.

The spatial and temporal distribution of catch and effort for the Soviet tuna purse-seine fishery in the Indian Ocean was determined from data in the YugNIRO database, a collection of daily radio reports from vessels fishing in the area from 1983 until the mid-1990s.[10] The catches reported by the author's estimates varied by 96–99% during 1985–91, decreasing to 71% in 1992. This study did not take into account reflagging of some Soviet (from 1992—Russian) vessels with the Liberian flag, and the vessels' nationality was defined in this study by the location of their shipowners. Analysis of fleet activity and extrapolations of results were made on the assumption that the operations and procedures on vessels that did not carry observers did not differ from the operations and procedures on vessels with an observer aboard; similarly it was assumed that the species composition of the catch from these vessels did not differ.

Some of the bycatch was retained on board the fishing vessels. Unused bycatch was discarded in the ocean. The observers usually did not record the levels of discards, and it was not possible to assess quantitatively the discards of tuna and associated species.

Average values are presented as arithmetic means, plus or minus 95% confidence intervals for estimated values. Estimates of unrecorded bycatches for all fishes, except tunas, are provided in numbers and metric tons per positive set and per 1000 t of target species.

Results

Primary data and adequacy of samples

A total of 494 purse-seine sets were sampled and 377 positive sets were analyzed. The total catch in the sets that were sampled amounted to 7713 t. The distribution of sets sampled by years, seasons, and the types of schools is given in Tables 1 and 2. The catch sampled by type of school is presented in Table 3.

The observer coverage rate varied from 0% (no observers at sea) to 75% and averaged 14% during 1986–92. During the periods when observers were on board, the coverage rate averaged 30% and varied from 5% to 75%. The spatial distribution of sampled sets agreed quite well with

[10] Daily information on fishing activity of these vessels in the Indian Ocean in 1983–84 and since 1995 is not available.

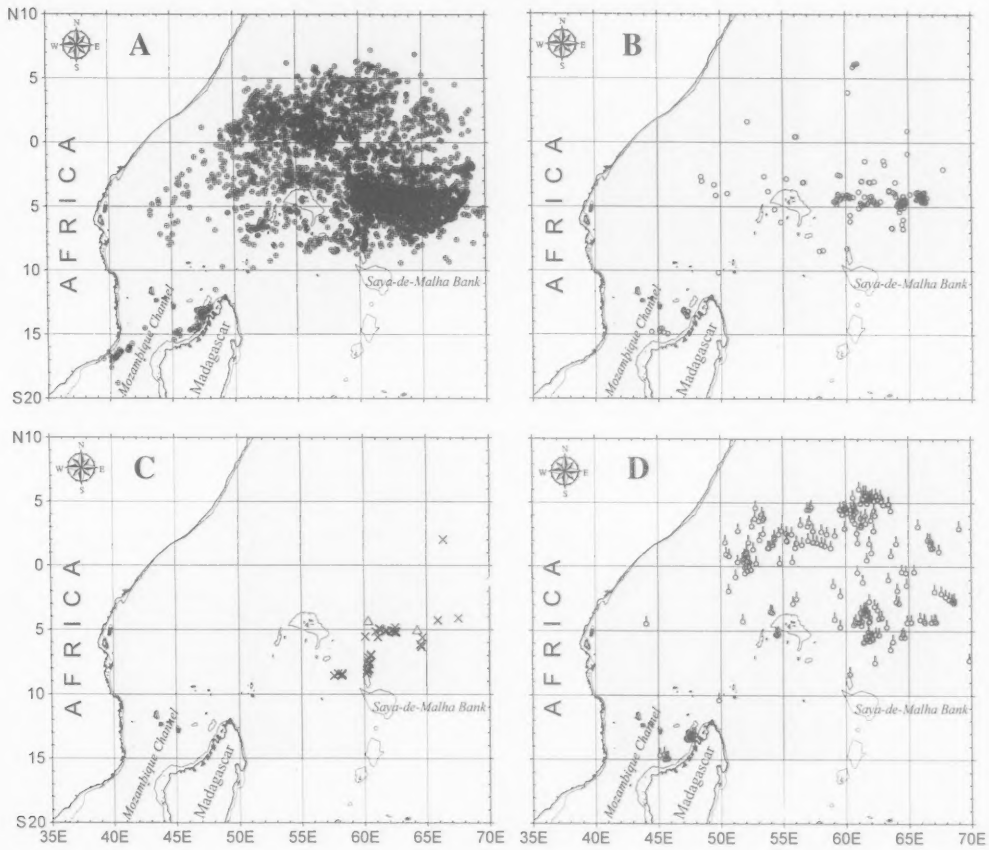

Figure 1

(**A**) Fishing effort distribution (⊗=noon positions of vessels on fishing days with sets) of the Soviet tuna purse-seine fishery in 1985–94; (**B–D**) sampled set positions: (B) on free-swimming schools that were sampled; (C) on whale-shark (△) and whale-associated schools (×); (D) on log-associated schools. The shaded area represents the region of the main international tuna purse-seine fishing activity in the WIO, according to Ardill.[11]

Table 3

Sampled catch (metric tons) by season and type of school.

	Seasons				
Type of school	Winter	Spring	Summer	Autumn	Total
Free-swimming	1884	249	73	24	2230
Whale-shark–associated	28	0	0	0	28
Whale-associated	584	467	4	0	1055
Log-associated	925	785	1156	1534	4400
Total	3421	1501	1213	1558	7713

the distribution of the total fishing effort of the Soviet fleet in the WIO (Fig. 1). Sampled sets were distributed throughout the region of the principal international tuna purse-seine fishing activity in the WIO (Ardill[11]). Thus, I

[11] Ardill, J. D. 1995. Atlas of industrial tuna fisheries in the Indian Ocean (IPTP/95/AT/3). IPTP, Colombo, Sri Lanka, 138 p. FAO, Viale delle Terme di Caracalla, 00100, Rome, Italy.

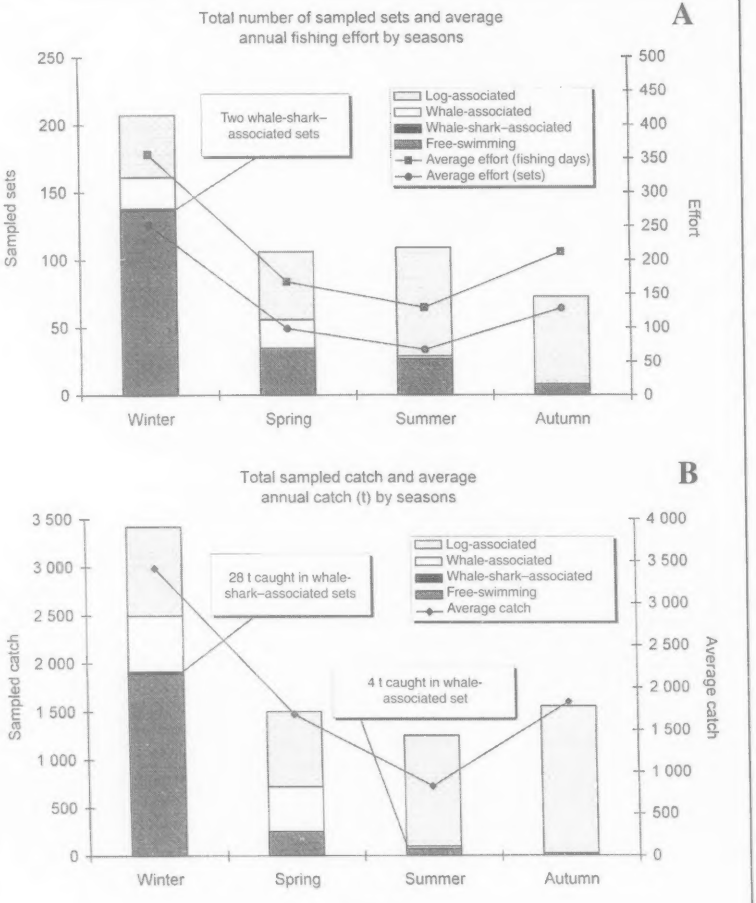

Figure 2

(**A**) Sampled effort (by school type) and the long-term average fishing effort by season; (**B**) sampled catch (by school type) and long-term average catch by season for the Soviet tuna fleet.

believe that the observers' data are representative of the catch by the Soviet purse-seine fleet in terms of sample size and geographical distribution of the sets.

The data series available for analysis was a combination of samples different in size, obtained in different years and seasons (Tables 1–3). Therefore the results of all analyses may have been subject to interannual variability (it is impossible to evaluate the effect of interannual variability from the data available), and the estimated average annual figures may have been subject to seasonal variability as well, on account of the unequal size of samples taken in different seasons.

Because the daily radio reports, which formed the basis of the database, did not include information on sets by school type, it was not possible to directly extrapolate the observers' data to the Soviet fleet separately by school types. However, I believe that the observers' data correctly reflect the seasonal ratio of sets on different school types.

To assess the possibility of using annual averages of the available samples and extrapolating them to the whole catch of the Soviet fleet, the author compared the seasonal magnitudes of total fishing effort (fishing days, sets) and catches reported by the Soviet fishing fleet (from the database) with the seasonal magnitudes of effort (number of sets) and catch (t) sampled by the observers (Fig. 2, A and B). The seasonal distribution of the sampled catch followed the same pattern as the long-term average seasonal distribution of the catch by the fleet (Fig. 2B). The effort did not fully agree with seasonal increase in the fishing effort of Soviet vessels during the autumn season (Fig. 2A), which may have resulted in a slight underestimation of average annual values of bycatch from log-associated

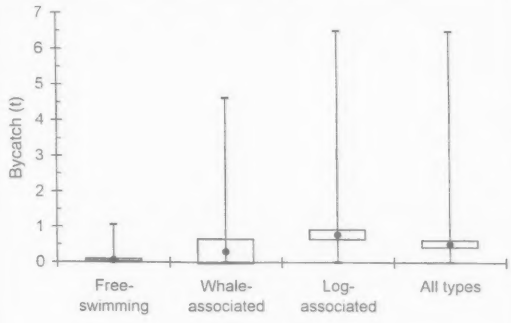

Figure 3

Bycatch per positive set in metric tons (t) by school type for the Soviet tuna purse-seine fishery. Dots are means, bars show range, and boxes are 95% confidence intervals.

schools. I did not attempt, however, to take this factor into consideration.

The average CPUE (e.g. total catch per set) in the purse-seine tuna fisheries varies greatly by type of vessel. I did not find a strong correlation between the bycatch per set and the total catch, or catch of target species in the same set. Level of bycatch generally depends on the type of association and the total fishing effort directed at this type of association.

Species composition and catch by school types

A total of 50 species (or higher taxa) of fishes and other marine animals were recorded in the catch of the fishing vessels (Table 4).

Free-swimming schools

Free-swimming schools are the predominant type of surface schools in the WIO. Such schools occurred in the area all year round (Table 2, Fig. 2, A and B). Soviet purse seiners set on free-swimming schools generally south of the equator (including Mozambique Channel)(Fig. 1B). Yellowfin, skipjack, and bigeye (*Thunnus obesus*) tunas were the principal components of free-swimming schools, comprising 80%, 15%, and 4%, respectively (Table 5). Monospecific (nonassociated) tuna schools, consisting completely of yellowfin or skipjack tuna, were found to occur in 47% of free-school sets. Multispecies free schools were observed in 53% of all free-school sets and generally consisted of two target species and bycatch. Bycatch occurred in 45% of the free-school sets, and nontuna bycatch in 22%.

A total of 19 species (or higher taxa of fishes) were observed in catches on free schools (Table 4). Some species were considered to be tuna prey (e.g. Exocoetidae) and some to be accidental bycatch (e.g. *Gempylus serpens, Canthidermis maculatus, Diodon* spp.). Nontuna bycatch in this type of association was on average 0.060 ±0.031 t per positive set (Fig. 3) and 3.403 ±2.770 t per 1000 t of target species (Fig. 4). The bulk of this bycatch was sharks of the genus *Carcharhinus* (0.023 t/1.296 t), rays of the Mobulidae family (0.020 t/1.128 t), marlins of the genus *Makaira*, and sailfish (*Istiophorus platypterus*) (0.016 t/0.895 t) (Tables 4 and 6). In the present study, bycatches are presented in parentheses as t per positive set/t per 1000 t of target species.

Whale-shark–associated schools

Two schools associated with whale sharks were sampled only in the winter season (Table 2, Fig. 2, A and B) south of the equator (Fig. 1C). In these sets, the bycatch consisted of the shark itself and a small quantity of albacore (*Thunnus alalunga*) (Table 4). This small sample size prohibited reliable bycatch estimates for whale-shark–associated schools and inferences of the species compositions of such associations.

Whale-associated schools

In the observers' logbooks, among the 45 sets on whale-associated tuna schools, 13 sets were made on schools associated with sei whales (*Balaenoptera borealis* Lesson, 1828) and one set on a school associated with a fin whale (*B. physalus* (Linnaeus, 1758)).[12] The remaining sets were made on unidentified baleen whales. According to verbal reports by some observers,[13] tuna schools associated with Bryde's whale (*B. edeni* Anderson, 1878), Minke whales (*B. acutorostrata* Lacépède, 1804), and pygmy blue whales (*B. musculus brevicauda* Linnaeus, 1758) were also observed in the WIO. From personal observations and those of the observers, sperm whales (*Physeter catodon* Linnaeus, 1758) were found often in the areas of the tuna purse-seine fishery; tunas, on the other hand, were not observed to associate with sperm whales. According to observations made during setting and searching operations, whales associated with tunas generally were found in groups of up to 8 individuals, more often in groups of 2–3 whales.

Whale-associated schools were most often observed from January to April. A whale-associated school was observed in July north of the equator (Table 2, Figs. 1C, 2, A and B). Schools of this type were distributed mainly south of the equator at latitudes 4–9°S. Skipjack, yellowfin, and bigeye tunas dominated in whale-associated schools—59%, 32%, and 6%, respectively (Table 5). The percentage of each species in different sets varied greatly: 0–100% for skipjack, 0–100% for yellowfin, and 0–74% for bigeye tuna. Associations consisting of one tuna species and a whale were encountered in eight cases (22%). Bycatch in whale-associated schools was found in 68% of the sets, and nontuna bycatch in 43% of the sets.

During sets on whale-associated schools, the fishermen keep the whale(s) inside the purse seine as long as pos-

[12] Species identification could be erroneous.

[13] Bashmakov, V. F. 1990. Personal commun. Atlantic Scientific Research Institute of Marine Fisheries and Oceanography (AtlantNIRO), 5 Dmitry Donskoy St., Kaliningrad, 236000, Russia.

Table 4

Species composition of tuna purse-seine catches in the western Indian Ocean. "?" denotes doubtful, in the author's opinion, species identification by observer.

	School type		
Family and species	Free-swimming	Whale-associated	Log-associated
Pisces			
Dasyatidae			
Dasyatis spp.	+		+
Mobulidae			
Manta birostris (Donndorff, 1798)	+?	+?	+
Mobula spp.	+	+	+
Rhincodontidae			
Rhincodon typus Smith, 1828[1]			
Lamnidae			
Isurus oxyrinchus Rafinesque, 1809		+	
Isurus spp.		?	
Carcharhinidae			
Carcharhinus falciformis (Bibron, 1839)	+	+	+
C. longimanus (Poey, 1861)	+	+	+
?C. obscurus (LeSueur, 1818)		+?	+?
Carcharhinus spp.		?	?
Sphyrnidae			
Sphyrna lewini (Griffith & Smith, 1834)			+
Sphyrna spp.			+
Exocoetidae sp.	+		
Belonidae sp.			+
Tylosurus crocodilus (Peron & LeSueur, 1821)			+
Lampidae			
Lampris guttatus (Brünnich, 1788)			+
Sphyraenidae			
Sphyraena barracuda (Walbaum, 1792)			+
Sphyraena spp.			+
Carangidae			
Caranx spp.			+
Decapterus macarellus Cuvier, 1833			+
Decapterus spp.			+
Elagatis bipinnulata (Quoy & Gaimard, 1824)	+		+
Seriola spp.	+		+
Naucrates ductor (Linnaeus, 1758)			+
Coryphaenidae			
Coryphaena hippurus Linnaeus, 1758		+	+
Coryphaena spp.			+
Kyphosidae			
Kyphosus cinerascens (Forsskål, 1775)			+
Gempylidae			
Gempylus serpens Cuvier, 1829	+		
Ruvettus pretiosus Cocco, 1829			+
Ephippididae			
Platax spp.		+	+
Scomberomoridae			
Scomberomorus commerson (Lacépède, 1800)			+
Scomberomorus spp.			+
Scombridae			
Acanthocybium solandri (Cuvier, 1831)			+

continued

Table 4 (continued)

Family and species	School type		
	Free-swimming	Whale-associated	Log-associated
Pisces (continued)			
Auxis rochei (Risso, 1810)			+
Auxis thazard (Lacepede, 1800)	+	+	+
Euthynnus affinis (Cantor, 1849)			+
Katsuwonus pelamis (Linnaeus, 1758)	+	+	+
Thunnus alalunga (Bonnaterre, 1788)	+		+
Thunnus albacares (Bonnaterre, 1788)	+	+	+
Thunnus obesus (Lowe, 1839)	+	+	+
Istiophoridae			
Istiophorus platypterus (Shaw & Nodder, 1792)	+		
Makaira indica (Cuvier, 1832)		+	+
M. mazara (Jordan et Snyder, 1901)	+		+
Makaira spp.	+		+
Tetrapturus audax (Philippi, 1887)			+
Xiphiidae			
Xiphias gladius (Linnaeus, 1758)			+
Nomeidae			
Cubiceps pauciradiatus Günter, 1872		+	
Balistidae			
Canthidermis maculatus (Bloch, 1786)	+		+
Monacanthidae			
Aluterus monoceros (Linnaeus, 1758)			+
Aluterus spp.			+
Diodontidae			
Diodon spp.	+		+?
Mammalia			
Balaenopteridae			
Balaenoptera borealis Lesson, 1828		+	
Salpae		+	
Ctenophora		+	
Chelonidea			+
Number of species (taxa)	19	17	45

[1] Recorded in whale-shark–associated schools.

Table 5

Average tuna catch per positive set (t) by "Rodina"-type Soviet vessels in the western Indian Ocean (total and by species). YFT = yellowfin tuna, SKJ = skipjack tuna, BET = bigeye tuna, ALB =albacore, FRI = frigate tuna, KAW = kawakawa. + = catch was <0.001 t.

Type of school	Total	Species					
		YFT	SKJ	BET	ALB	FRI	KAW
Free-swimming	18.4 ±5.2	14.7 ±4.9	2.8 ±1.7	0.8 ±1.0	0.03 ±0.03	0.05 ±0.06	—
Whale-associated	31.0 ±9.3	9.8 ±4.3	18.3 ±8.5	2.0 ±2.4	—	0.2 ±0.2	—
Log-associated	20.6 ±3.2	4.9 ±0.9	13.9 ±2.7	0.6 ±0.2	0.04 ±0.04	0.3 ±0.3	0.001 ±0.001
Total	20.6 ±2.7	8.6 ±1.8	10.5 ±1.9	0.8 ±0.4	0.03 ±0.03	0.2 ±0.2	+

Table 6

Estimates of the bycatch (t) of various species (groups) of marine animals by school type. The numerator is the average values per a positive set, the denominator is the average values per 1000 t of target species. + = catch was <0.001 t.

Species or group of species	School type[1]			
	Free-swimming	Whale-associated	Log-associated	All types of schools
Billfishes (Istiophoridae, Xiphiidae)	0.016/0.895	0.006/0.218	0.019/1.008	0.017/0.880
Wahoo (*A. solandri*)	—	—	0.031/1.621	0.018/0.934
Sharks (Lamnidae, Carcharhinidae, Sphyrnidae)	0.023/1.296	0.289/10.302	0.175/9.288	0.151/7.938
Rainbow runner (*E. bipinnulata*)	0.001/0.054	—	0.195/10.314	0.114/5.962
Dolphinfishes (*C. hippurus*)	+/0.027	0.001/0.051	0.191/10.098	0.111/5.836
Barracuda (*S. barracuda*)	—	—	0.002/0.132	0.001/0.076
Triggerfishes (*C. maculatus, Aluterus* spp.)	+/+	—	0.137/7.277	0.080/4.195
Mackerel scad (*D. macarellus*)	—	—	0.0093/0.491	0.005/0.283
Mantas, mobulas (Mobulidae)	0.020/1.128	0.009/0.318	0.002/0.126	0.009/0.455
Sea turtles	—	—	+/0.025	+/0.014
Other bycatch	+/0.002	+/0.003	0.018/0.958	0.011/0.553
Total { For positive set	0.060 ±0.031	0.306 ±0.344	0.780 ±0.144	0.518 ±0.099
Total { For 1000 t of target species	3.403 ±2.770	10.891 ±15.787	41.337 ±14.281	27.127 ±8.869

[1] Because of the small sample size, estimates of bycatch for whale-shark–associated schools are not presented in the Table.

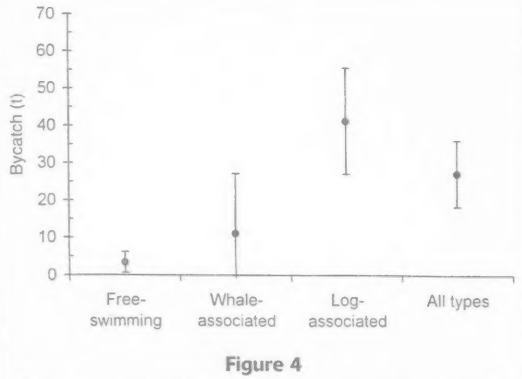

Figure 4

Bycatch (t) per 1000 t of target species by school type for the Soviet tuna purse-seine fishery. Dots are means, bars are 95% confidence intervals.

sible. Whales often remain in the net until the end of pursing and then escape from the purse seine by either diving under the purse line, by ramming through the net wall, or by sinking the corkline (a rare occurrence).

Observers registered a single case of entanglement in the net and subsequent death of a young sei whale about 10 m in length and about 12 t in weight. The dead animal was taken up on the vessel's deck, released from the purse seine, and discarded into the ocean. It is not possible to assess the frequency and probability of whale mortality by the purse-seine fishery in the WIO.

There were 17 species (or groups) of marine animals identified in the catches of whale-associated schools (Table 4). Salps, ctenophores, and batfish (*Platax* spp.) were considered accidental bycatch, whereas long-finned fathead (*Cubiceps pauciradiatus*) was a prey item of both tunas and whales. Nontuna bycatch in this type of association averaged 0.306 ±0.344 t for a positive set or 10.891 ±15.787 t per 1000 t of target species (Figs. 3 and 4). Sharks of the genus *Carcharhinus* and *Isurus* made up the bulk of the bycatch in whale-associated school sets (0.289 t/10.302 t) (Tables 4 and 6).

Log-associated schools

Log-associated schools are one of the predominant school types found in the WIO all year round (Table 2, Fig. 2, A and B). Sets on log-associated schools were made throughout the sampling area as far south as 15°S (Fig. 1D). In log-associated schools the bulk of the catch were skipjack, yellowfin, and bigeye tunas—67%, 24%, and 3%, respectively (Table 5). Log-associated schools in all cases consisted of several fish species. Bycatch was found in 93% of the sets, and nontuna bycatch in 87%. The absence of bycatch was rare, observed only during successive sets on the same floating object.

The species composition associated with floating objects was the most diverse of any set type and included 45 species (or higher taxa of fishes) (Table 4). Nontuna bycatch was at its highest in log-associated sets, as much as 0.780 ±0.144 t per positive set or 41.337 ±14.281 t per 1000 t of target species (Figs. 3 and 4). The bulk of the bycatch in sets on log-associated schools was made up of rainbow runner,

Elagatis bipinnulata (0.195 t/10.314 t), common dolphinfish, *Coryphaena hippurus* (0.191 t/10.098 t), triggerfish of the genus *Canthidermis* (0.137 t/7.277 t), sharks of the genus *Carcharhinus* (0.175 t/9.288 t), wahoo, *Acanthocybium solandri* (0.031 t/1.621 t), billfishes of the genera *Makaira* and *Tetrapturus* (0.019 t/1.008 t), and mackerel scad, *Decapterus macarellus* (0.0093 t/0.491 kg). One capture of a sea turtle (unknown species) was recorded (Tables 4 and 6).

All types of schools

Considering all school types in the aggregate, skipjack, yellowfin, and bigeye tuna prevailed in the catch —51%, 42%, and 4% by weight, respectively (Table 5). Albacore represented a mere 0.2%, frigate tuna 0.9%, and kawakawa, *Euthynnus affinis*, less than 0.1%. Nontuna bycatch accounted for less than 3% of the catch.

On the average, there was 0.518 ±0.099 t of nontuna bycatch caught per positive set, or 27.127 ±8.869 t per 1000 t of target species (Fig. 3). Bycatch levels by species (groups) are given in Table 6.

Discussion

The lowest fish bycatch in the WIO tuna purse-seine fishery was taken from free schools (mainly carcharhinid sharks and Mobulidae rays) (Figs. 3 and 4, Tables 4 and 6). Bycatch of fishes was highest and most diverse from catches on log-associated schools. Rainbow runner, common dolphinfish, triggerfish, carcharhinid sharks, wahoo, billfishes, and mackerel scad were predominant. Whale-associated schools were characterized by an intermediate level of bycatch (mainly carcharhinid and lamnid sharks) (Figs. 3 and 4, Tables 4 and 6).

It is interesting to compare the bycatch rates obtained in this study with those published for other regions. The principal bycatch fishes in the Pacific (Bailey et al., 1996; Hall, 1996, 1998; Anonymous, 1997) are the same as those presented here. Bycatch levels are known to vary considerably by year, area, fleet (Bailey et al., 1996; Hall, 1996; Anon., 1997), and school type; this variability hampered direct comparisons of the results from the present study with those from published data. However, for the purpose of comparison, I pooled my estimates by groups in accordance with the published data (Bailey et al., 1996; Hall, 1996, 1998; Anonymous, 1997). Bycatch levels per set and per 1000 t of target species for various regions of the Pacific and my estimates for the Indian Ocean are on the same order of magnitude for most groups in similar types of associations (Figs. 5 and 6).

I also attempted to estimate the unrecorded bycatch by the purse-seine fleets of the principal fishing nations of the WIO by a comparison of fishing tactics. The Soviet fleet in the WIO made an equal proportion of sets on free-swimming schools and on log-associated schools during the year (Table 2). Seasonally they switched effort from sets on free-swimming schools to those on log-associated schools (Fig. 7, A and B). The fishing practices of French and Spanish tuna seiners showed similar seasonality until the mid-1990s (Anonymous;[14,15,16] Pianet;[17,18] Moron[19]).

The fishing tactics of the Japanese (Hallier;[20] Okamoto and Miyabe[21]) and Mauritian (Norungee et al.;[22] Norungee and Lim Shung[23]) purse-seine fleets differed considerably from that described above. Japanese and Mauritian vessels made sets on log-associated schools all year round, with single instances of sets on other schools types.

Only two school types (log schools and free schools) have been described by Hallier;[20] Hallier;[24] Parajua Aranda;[25]

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Table 7

Bycatch estimates in tons in the western Indian Ocean purse-seine fisheries during 1985–94. MIX = fleets targeted all types of schools (France, Spain, USSR), LOG = fleets targeted log-associated schools (Japan and Mauritius).

Species, a group of species		1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
	MIX	913	1047	1257	1674	1622	1503	1471	1793	1796	1925
Pelagic oceanic sharks	LOG	31	30	61	81	108	180	278	477	451	143
	Total	944	1077	1318	1755	1730	1683	1749	2270	2247	2068
	MIX	686	786	944	1257	1218	1129	1105	1347	1349	1446
Rainbow runners	LOG	34	33	68	90	120	199	309	530	500	159
	Total	720	819	1012	1347	1338	1328	1414	1877	1849	1605
	MIX	671	770	925	1231	1193	1105	1082	1318	1320	1415
Dolphinfishes	LOG	34	33	67	88	117	195	303	518	490	156
	Total	705	803	992	1319	1310	1300	1385	1836	1810	1571
	MIX	483	554	665	885	857	794	778	948	949	1017
Triggerfishes	LOG	24	24	48	64	84	141	218	374	353	113
	Total	507	578	713	949	941	935	996	1322	1302	1130
	MIX	108	123	148	197	191	177	173	211	211	227
Wahoo	LOG	5	5	11	14	19	31	49	83	79	25
	Total	113	128	159	211	210	208	222	294	290	252
	MIX	101	116	139	185	180	167	163	199	199	213
Billfishes	LOG	3	3	7	9	12	20	30	52	49	16
	Total	104	119	146	194	192	187	193	251	248	229
	MIX	52	60	72	96	93	86	84	103	103	110
Mobulas and mantas	LOG	<1	<1	1	1	1	2	4	6	6	2
	Total	53	60	73	97	94	88	88	109	109	112
	MIX	33	37	45	60	58	54	53	64	64	69
Mackerel scad	LOG	2	2	3	4	6	10	15	25	24	8
	Total	35	39	48	64	64	64	68	89	88	77
	MIX	9	10	12	16	16	14	14	17	17	19
Barracudas	LOG	<1	<1	1	1	1	3	4	7	6	2
	Total	9	11	13	17	17	17	18	24	23	21
	MIX	64	73	88	117	113	105	102	125	125	134
Other fishes	LOG	3	3	6	8	11	18	29	49	47	15
	Total	67	76	94	125	124	123	131	174	172	149
	MIX	3120	3576	4295	5718	5541	5134	5025	6125	6135	6574
Total nontuna bycatch	LOG	137	134	273	360	479	799	1239	2121	2004	638
	Total	3257	3710	4568	6078	6020	5933	6264	8246	8139	7212

Anonymous;[14, 15, 16] Pianet;[17, 18] Hastings and Domingue;[26] and Moron[19] for the tuna purse-seine fishery in the Indian Ocean. Free schools in these analyses included all types of associations with marine animals. The proportion of sets of the French fleet on other types of schools and on resulting catches is not known. Cort (1992) presented such data for Spanish vessels, based on fishing logbooks. Therefore, I used the observers data of the Seychelles Fishing Authority (SFA) (Cort, 1992) for the vessels of France, Spain, Japan, and USSR to assess these values in the WIO. The percentage of sets on whale-associated schools varied from 1.7% to 8.8% in 1986–90, the percentage among positive sets was from 1.2% to 9.1%, and the catch from such schools was 1.6% to 7.8% (cited from Cort, 1992). These values are slightly lower than the observer data I report in the present study (9%, 10%, and

[24] (continued) Proceedings of the expert consultation on Indian Ocean tunas, 5th session, Mahe, Seichelles, 4–8 October, 1993 (J. D. Ardill, ed.), p. 192–198. IPTP Coll. Vol. 8., TWS/93/2/25. FAO, Viale delle Terme di Caracalla, 00100, Rome, Italy.

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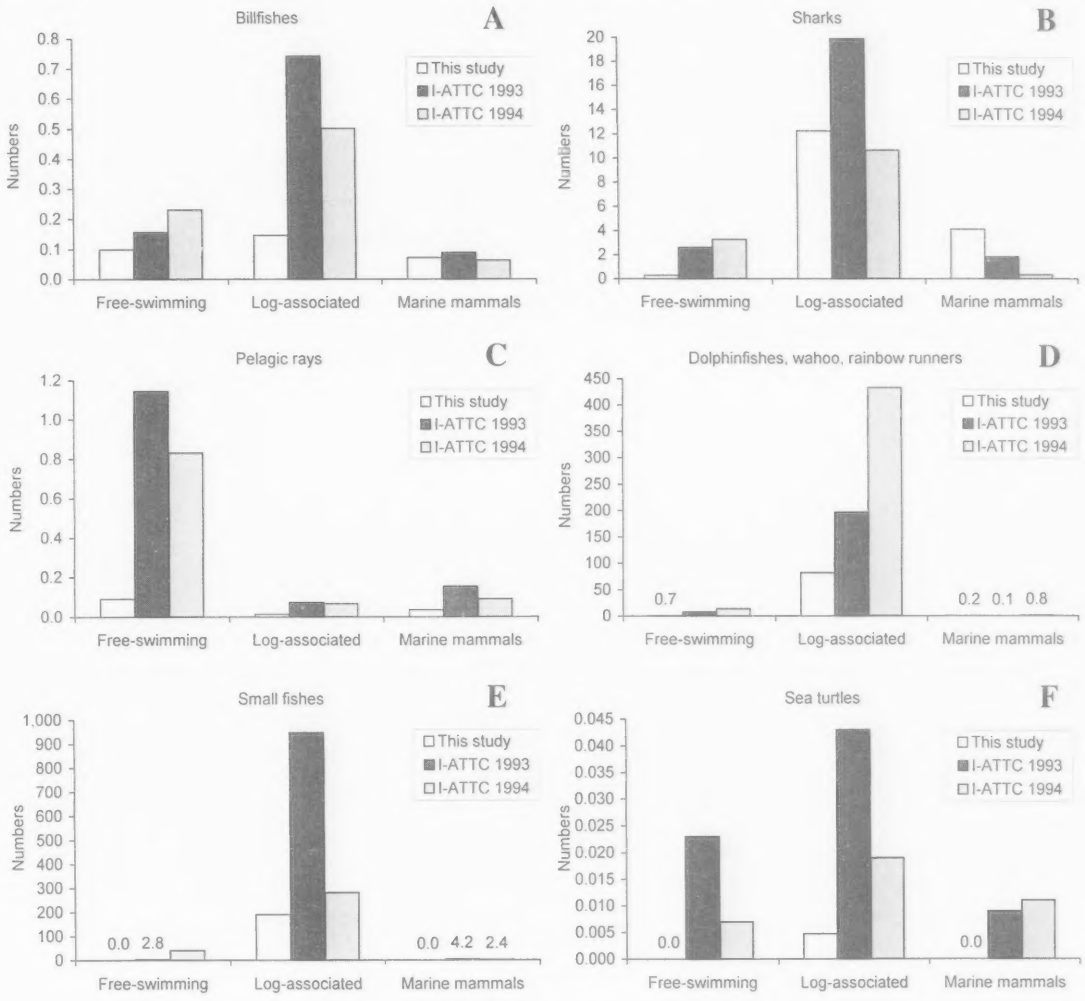

Figure 5

Bycatch levels in numbers per set by groups of species and by types of schools in the western Indian Ocean and eastern Tropical Pacific (Anonymous, 1997).

14%, respectively), which is explained by the fact that the SFA data included Japanese vessels known to fish on log-associated schools only. Nevertheless, the SFA values and those from our observers were on the same order of magnitude. Proceeding from this, I estimated the ratio of sets on various school types and the magnitude and species composition of bycatch by the French and Spanish vessels. These values were close to those for the Soviet fleet employing similar fishing tactics.[27]

Thus, the average bycatch estimates presented in this study can be extrapolated for this period to the total WIO purse-seine catch of principal fishing nations targeting all types of schools.[28] Estimates of bycatch from log-associated schools, I believe, can be extended, with some caution, to the pooled purse-seine catch of Japan and Mauritius in the WIO.

The annual purse-seine catches of yellowfin and skipjack tunas by fleets targeting all types of schools (France,

[27] Data from logbooks (Cort, 1992) show a lower proportion of sets and of catches on whale-associated schools for Spanish vessels, but in the author's view a comparison of data collected in the same way (by observers) is preferable.

[28] France and Spain (along with catch from the vessels from these two countries flying "flags of convenience" [Panama, Côte d'Ivoire, and recently Belize] and applying the same fishing tactics), and USSR (recently Russia or Liberia).

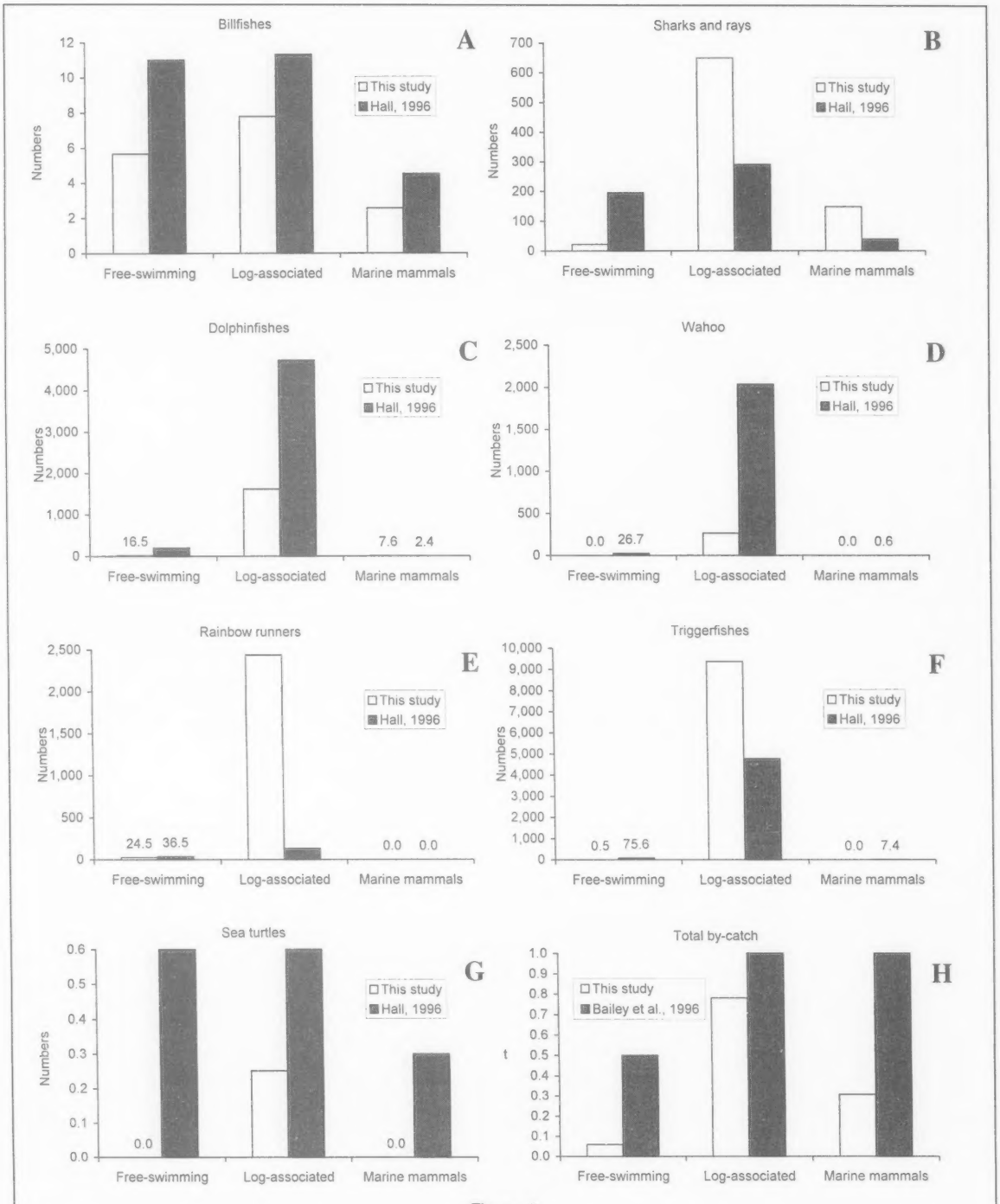

Figure 6

(**A–G**). Bycatch levels, in numbers per 1000 t of target species, by groups of species and by types of schools in the western Indian Ocean and eastern Tropical Pacific; (**H**) bycatch levels, in tons per set by types of schools in the western Indian Ocean and western Pacific Ocean.

Spain, and USSR)[29] in the WIO ranged between 115,000 and 242,000 t in 1985–94 (Anonymous[30]). Japanese and Mauritian catches varied from 3000 to about 51,000 t. Based on these values, the estimated bycatch was 3257 to 8246 t of various fishes during the same period (Table 7). These fishes could serve as food for the coastal countries of the area. Estimated bycatch in numbers is presented in Table 8.

Turtle bycatch and whale mortality in purse seines are also possible in the WIO, but the probability of the latter is very low. No instances of whale mortality have been recorded earlier for tuna purse-seine fisheries in other areas (Northridge, 1984, 1991a, 1991b; Medina-Gaertner and Gaertner, 1991; Santana et al., 1991; Cort, 1992; Cayre et al., 1993; Bailey et al., 1996). No avian mortality by the Soviet tuna purse-seine fishery has been noted by observers. A similar fact was reported for the western Pacific (Bailey et al., 1996).

Target fishing for rainbow runner, dolphinfish, triggerfishes, wahoo, mackerel scad, and barracuda is not conducted in the WIO, and these fish are taken only as bycatch. Their bycatch levels, estimated in this study, do not seem to endanger the populations of these species.

Estimated bycatch of billfishes (104–251 t annually) was less than 1% of the total catch for these species (14,000–33,000 t during 1985–94) in the WIO (Anonymous[30]). The bycatch by the purse-seine fishery was unlikely to substantially affect the billfish stocks.

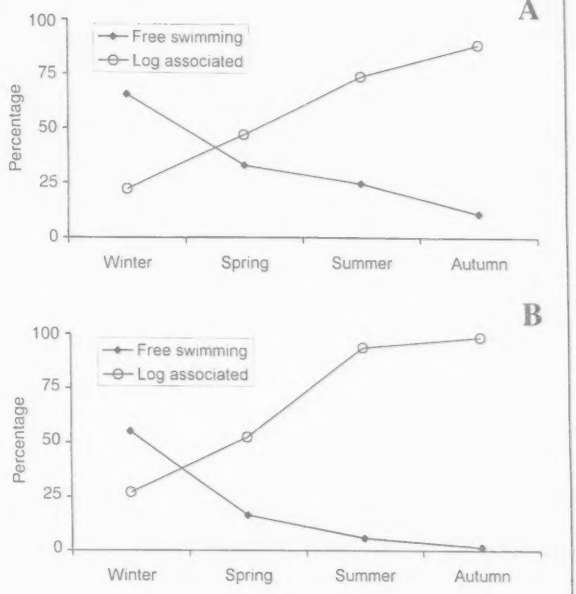

Figure 7

(**A**) Percentages of free-school and log-schools sets; (**B**) percentages of free-school and log-school catch in the Soviet tuna purse-seine fishery.

Many pelagic sharks are taken as bycatch by the longline, trawl, coastal driftnet, and other fisheries, but are not recorded. The total shark catch by all fisheries may be considerable. Many shark species are characterized by low abundance, low fecundity, long life span, and consequently, by high vulnerability to overfishing. Underestimation of the removal through fisheries of a number of pelagic shark species, and the impact of the fisheries on their populations, may lead to a reduction in their abundance to critical levels, diminishing the biodiversity of the pelagic ecosystem of the Indian Ocean.

Some part of the bycatch is released into the ocean alive, although subsequent survival rates are unknown. The lack of bycatch and discard records and estimates of survival rates of discarded animals prevents assessment of the impact of the fishery on the Indian Ocean pelagic ecosystem.

Fishing tactics in the WIO have changed considerably by all principal purse seine fleets toward the extensive use of FADs in recent years (generally from 1995). The majority of Japanese vessels have left the area and have moved to the eastern Indian Ocean. Therefore estimates presented here for total WIO purse-seine fisheries are applicable for a limited time span only (pre-1995). Recent development of the WIO fisheries warrants further investigation of bycatches through extensive observer sampling by time–area strata.

Establishing a scientific program by the Indian Ocean Tuna Commission to monitor the principal tuna fisheries in the region, by placing international scientific observers on purse-seine and longline vessels, might be the first step toward a more accurate assessment of the impact of bycatches on the epipelagic ecosystem of the Indian Ocean. This program might also lead to developing technical and management measures to reduce the bycatches or to use them.

The solution to the bycatch problem should take two directions: 1) an effort to reduce or eliminate bycatches of undesired species; or 2) to use bycatch animals to make them target species. The former involves developing gear modifications or changes in fishing tactics. The latter involves management regulation of the fishery so that bycatch species are treated in the same way as other target species.

Acknowledgments

I am grateful to AtlantNIRO scientists V. F. Bashmakov, G. A. Budylenko, V. Z. Gaikov, M. E. Grudtsev, to TINRO scientist K. A. Karyakin for their data made available to the author and to V. F. Bashmakov and G. A. Budylenko for their personal sampling efforts. I sincerely thank masters of the

[29] Including vessels flying flags of convenience.

[30] Anonymous. 1998. Indian Ocean tuna fisheries data summary, 1986–1996. Indian Ocean Tuna Commission (IOTC) data summary 18, 180 p. IOTC, P.O. Box 1011, Victoria, Seychelles.

Table 8

Bycatch estimates in numbers in the western Indian Ocean purse-seine fisheries during 1985–94. Codes are same as table 7. MIX = fleets targeted all types of schools (France, Spain, USSR); LOG = fleets targeted log-associated schools (Japan and Mauritius).

Species, a group of species		1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
Pelagic oceanic sharks	MIX	45,600	52,273	62,780	83,581	80,993	75,052	73,455	89,529	89,676	96,094
	LOG	2161	2100	4280	5653	7531	12,546	19,456	33,320	31,488	10,030
	Total	47,761	54,373	67,060	89,234	88,524	87,598	92,911	122,849	121,164	106,124
Rainbow runners	MIX	162,457	186,232	223,664	297,770	288,550	267,386	261,694	318,961	319,485	342,351
	LOG	8112	7883	16,065	21,218	28,267	47,090	73,029	125,065	118,190	37,646
	Total	170,569	194,115	239,729	318,988	316,817	314,476	334,723	444,026	437,675	379,997
Dolphinfishes	MIX	107,711	123,473	148,291	197,424	191,312	177,280	173,505	211,474	211,821	226,982
	LOG	5373	5221	10,641	14,053	18,723	31,190	48,370	82,835	78,282	24,934
	Total	113,084	128,694	158,932	211,477	210,035	208,470	221,875	294,309	290,103	251,916
Triggerfishes	MIX	621,823	712,823	856,096	1,139,747	1,104,458	1,023,450	1,001,661	1,220,857	1,222,862	1,310,387
	LOG	31,215	30,334	61,820	81,646	108,774	181,205	281,018	481,252	454,799	144,863
	Total	653,038	743,156	917,916	1,221,393	1,213,232	1,204,655	1,282,679	1,702,109	1,677,661	1,455,250
Wahoo	MIX	17,444	19,996	24,016	31,973	30,983	28,710	28,099	34,248	34,304	36,760
	LOG	876	851	1734	2290	3051	5083	7883	13,501	12,759	4064
	Total	18,320	20,847	25,750	34,263	34,034	33,793	35,982	47,749	47,063	40,824
Billfishes	MIX	750	859	1032	1374	1332	1234	1208	1472	1474	1580
	LOG	26	25	51	68	90	151	233	400	378	120
	Total	776	884	1083	1442	1422	1385	1441	1872	1852	1700
Mobulas and mantas	MIX	250	286	344	458	444	411	403	491	491	527
	LOG	3	2	5	7	9	15	23	39	37	12
	Total	253	288	349	465	453	426	426	530	528	539
Mackerel scad	MIX	45,134	51,739	62,138	82,726	80,164	74,285	72,703	88,613	88,758	95,111
	LOG	2266	2202	4487	5926	7895	13,153	20,398	34,931	33,011	10,515
	Total	47,340	53,941	66,625	88,652	88,059	87,438	93,101	123,544	121,769	105,626
Barracudas	MIX	1350	1547	1858	2474	2397	2221	2174	2650	2654	2844
	LOG	68	66	134	177	236	393	610	1044	987	314
	Total	1418	1613	1992	2651	2633	2614	2784	3694	3641	3158

KUTF tuna seiners A. G. Burlyko, V. N. Volvach, A. A. Kiryanov for their assistance rendered to observers in sampling.

The author is grateful to V. F. Demidov, N. N. Kukharev, M. A. Pinchukov, L. K. Pshenichnov, S. T. Rebik, B. G. Trotsenko for useful discussions when preparing the manuscript and to two anonymous reviewers for their comments and suggestions.

The author wishes to thank I. V. Charova for translating the paper into English. Revisions and an edition of the paper by R. J. Olson (I-ATTC) and his corrections of English were extremely valuable.

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Ontogenetic shifts in natural diet during benthic stages of American lobster (*Homarus americanus*), off the Magdalen Islands

Bernard Sainte-Marie
Denis Chabot

Division des invertébrés et de la biologie expérimentale
Institut Maurice-Lamontagne
Pêches et Océans Canada
850 route de la Mer
Mont-Joli (Qc), G5H 3Z4 Canada
E-mail address (for B. Sainte-Marie): Sainte-Marie@dfo-mpo.gc.ca

Abstract–The natural diet of 506 American lobsters (*Homarus americanus*) ranging from instar V (4 mm cephalothorax length, CL) to the adult stage (112 mm CL) was determined by stomach content analysis for a site in the Magdalen Islands, Gulf of St. Lawrence, eastern Canada. Cluster and factor analyses determined four size groupings of lobsters based on their diet: <7.5 mm, 7.5 to <22.5 mm, 22.5 to <62.5 mm, and ≥62.5 mm CL. The ontogenetic shift in diet with increasing size of lobsters was especially apparent for the three dominant food items: the contribution of bivalves and animal tissue (flesh) to volume of stomach contents decreased from the smallest lobsters (28% and 39%, respectively) to the largest lobsters (2% and 11%, respectively), whereas the reverse trend was seen for rock crab *Cancer irroratus* (7% in smallest lobsters to 53% in largest lobsters). Large lobsters also ate larger rock crabs than did small lobsters. This study is the first to examine the natural diet of shelter-restricted juveniles (SRJs, <14.5 mm CL), which were thought to be principally suspension feeders and to a lesser degree browsers or ambush predators in or near their shelter. However, at our study site no planktonic organisms were identified from the stomachs of SRJs, whereas formaniferans, crustacean meiofauna, and macroalgal debris that could be derived by browsing, together represented only 10–14% by volume of stomach contents. We infer that SRJs obtained bivalves by predation and flesh by exploiting larger lobsters' meal scraps or food reserves. Some implications of these findings for lobster artificial reef programs and for the conservation of lobster stocks are discussed.

Manuscript accepted 3 October 2001.
Fish. Bull. 100(1):106–116 (2002).

American lobster, *Homarus americanus*, is a long-lived, dominant predator in temperate coastal waters of eastern North America (Elner and Campbell, 1991; Ojeda and Dearborn, 1991). After the larval phase, lobsters settle and spend much of their time in burrows or natural shelters (Cobb, 1971; Lawton, 1987; Barshaw and Bryant-Rich, 1988). However, laboratory and *in situ* observations indicate that benthic lobsters pass through successive life-history phases as they grow in size, changing from a shelter-restricted habit to a more overt lifestyle involving daily forays and seasonal migrations away from shelter (Cooper and Uzmann, 1977; Cobb and Wahle, 1994). A variety of classifications have been proposed for these successive ontogenetic phases. The latest scheme, by Lawton and Lavalli (1995), recognizes five life-history phases: shelter-restricted juvenile (SRJ, ~4–14 mm cephalothorax length, CL), emergent juvenile (~15–25 mm CL), vagile juvenile (~25 mm CL to size of physiological maturity), adolescent, and adult.

In several decapod crustaceans, diet changes as individuals grow and become more mobile and their chela size and strength increases (e.g. Lee and Seed, 1992; Freire et al., 1996). Such dietary shifts should occur in the lobster as well, especially considering this species' changing dependency on shelter which, in turn, has implications for foraging range and accessibility of prey types (Elner and Campbell, 1987; Lawton, 1987). Some studies of the natural diet of lobsters 12–125 mm CL have found little or no differences in the identity or in the frequency of food items that were ingested by different size groups (Weiss, 1970; Ennis, 1973; Hudon and Lamarche, 1987). However, other studies have pointed to changes in the identity and especially in the frequency of food items ingested by different lobster size groups. Carter and Steele (1982b), using their own results and data from nonconcomitant studies conducted at different sites in Newfoundland (Squires, 1970; Ennis, 1973), have suggested that lobsters of 12–73 mm CL consume sea urchins, ophiuroids, and mussels more frequently than larger (adult) lobsters. Scarratt (1980) reported that lobsters consumed more crabs, mussels, and fish, but fewer echinoderms, as they grew in size and approached maturity. This trend was attributed to differential accessibility of prey. Elner and Campbell (1987) indicated that the stronger chelae of larger lobsters would enable them to crush prey that are protected by heavy shells, such as gastropods and bivalves, more so than the chelae of smaller lobsters.

The natural diet of SRJ lobsters has not been examined to date (Lawton and Lavalli, 1995), excepting rare specimens of 12–14 mm CL. The feeding appendages of SRJs are capable of capturing and processing both planktonic and benthic organisms (Lavalli and Factor, 1995). From laboratory observations, several authors have proposed that SRJs may live primarily as suspension-feeders, and to a lesser degree as browsers, within the shelter or as ambush predators at the shelter's entrance (Barshaw and Bryant-Rich,

1988; Barshaw, 1989; Lavalli and Barshaw, 1989; Lawton and Lavalli, 1995). Wahle (1992) offered a conceptual model suggesting that lobsters shift from a cryptic to a wide-roaming behavior as predation risk becomes offset by the need for a high-energy diet that cannot be satisfied through shelter-restricted feeding.

Our study was conducted at the Magdalen Islands, eastern Canada, to resolve the natural diet of SRJ lobsters and to compare it with that of larger lobsters by using stomach content analysis. We found a gradual ontogenetic shift in lobster diet over the size range of 4 to 112 mm CL. SRJs were carnivorous and probably derived their meals mainly through predation and scavenging. We also determined the predator-prey size relationship for one of the lobster's preferred and most important prey, i.e. Atlantic rock crab, *Cancer irroratus* (Reddin, 1973; Evans and Mann, 1977; Carter and Steele, 1982a).

Materials and methods

The study site was a narrow 2-km rocky section (47°14.5′N, 61°50.5′ to 61°51.3′W) of the south shore of Baie de Plaisance, Magdalen Islands, eastern Canada. This site corresponds to the Butte-à-la-Croix location that Hudon (1987) determined to be a settlement ground for lobster. Divers collected lobsters by hand or by suction-sampling at depths of 1 to 7 m. Lobsters were processed live usually within minutes and at most two hours after collection. The sex of collected specimens was determined and their CL was measured to the nearest 0.1 mm with a vernier caliper. Lobsters that were not berried and that were judged to be intermolt, based on criteria of shell hardness, coloration, and fouling in Aiken (1980), were dissected to remove the stomach which was preserved in buffered formalin diluted to 4% in seawater. Stomachs with calcified gastroliths were subsequently disregarded, thereby effectively eliminating from the present study all premolt lobsters from stage $D^{1.5}$ ($=D_0$) on (Aiken, 1980). The resulting sample consisted of 471 stomachs from lobsters of 7–112 mm cephalothorax length (CL) collected from 24 July to 31 October 1996, and of 35 stomachs from lobsters of 4–12 mm CL collected between 4 August and 13 September 1997. The 1997 lobsters were added to improve coverage of stomach contents of the early juveniles because very little settlement occurred in 1996 (Sainte-Marie et al., 2001). There was no commercial fishery during the sampling periods; therefore items in lobster stomachs were not discards or bait.

In the laboratory, stomachs were opened and their content was emptied into dishes for examination under a Wild M8 compound microscope (10–50×). Identity of food items was determined to the lowest taxonomic level possible, based on comparisons with illustrations in literature and samples of benthic and pelagic fauna from our study site. Particular care was taken when examining the stomach contents of lobsters <12 mm CL; for these stomach contents we often resorted to higher magnification (>100×) with a Leitz Dialux 20 microscope.

The contribution of each food item, exclusive of minerals and nylon debris, to the volume of stomach contents of each lobster was visually scored from 0 to 10, by 10% increments (0=0% of volume, 1=1–10%, 2=11–20%, etc.). The total for all food items could exceed 10, for example, if more than two minor food items each were scored 1 in addition to one predominant food item that was scored 8. In such cases, the corrected contribution of each food item was obtained by dividing its score by the sum of scores for all organic food items in a given stomach. Corrected volumetric contribution of each food item was expressed as a proportion of stomach content volume.

To obtain information on the size spectrum of rock crab consumed by lobsters, we established predictive (least squares) linear regressions (Sokal and Rohlf, 1995) between 30 measurements of distinctive hard body parts and cephalothorax width (CW) of 26 crabs ranging from 7 to 62 mm CW (following the approach in Lovrich and Sainte-Marie, 1997). All the predictive regressions were highly significant (r^2=0.970–0.999, P<0.001). When rock crab remains were encountered in lobster stomachs, distinctive hard body parts were measured with an eyepiece micrometer to estimate crab CW from predictive regressions. When more than one body part could be measured, the crab's CW was determined as the mean of the various estimates unless it was obvious that multiple crabs had been ingested. Such was considered to be the case when more than two similar fragments of a paired structure (e.g. eyes or claws) were found in one lobster stomach or when there was considerable divergence among crab CW estimates based on different body parts. The functional relationship between the CW of rock crab prey and the CL of lobster predators was established with a model II regression (Laws and Archie, 1981; Sokal and Rohlf, 1995).

The stomach contents, once identified and scored for volume, were transferred separately to preweighed trays, dried to constant mass at 60°C, and weighed to the nearest mg. Dry mass was not obtained for eight stomach contents because of manipulation errors. The allometric relationship between the dry mass of stomach contents and lobster CL was established by least squares linear regression, after logarithmic transformation of both variables.

Diet was described by occurrence, volumetric contribution, and the specific abundance of food items in the stomachs of lobsters grouped into 5-mm CL size classes (2.5 to <7.5 mm, 7.5 to <12.5 mm, etc.). Percent occurrence (PO) was the percentage of stomachs in one size class that contained a given food item. Volumetric contribution (VC) was the average of corrected contributions of each food item to the stomachs of all lobsters in a given size class. Specific abundance (SA) was the average volumetric contribution of a food item determined only for lobsters that had this food item in their stomach. This index is useful for food items with a low average volumetric contribution because it allows the distinction between the case when few animals consume large quantities of a given food item or when many animals consume small quantities of the same food item (Amundsen et al., 1996). The mathematical relationship of the three indices is $SA = VC \times 100/PO$.

To assess how the overall diet varied with lobster size, and thus whether or not there were size-related shifts in diet supporting the ontogenetic phases of lobster, we

performed a cluster analysis (Ward's minimum variance method) on the volumetric contribution of food items per lobster size class, after standardization. A sudden increase in the joining distance of the clustering sequence represented by the dendrogram represents a natural cutting point for the determination of meaningful clusters (SAS Institute, 1995). In addition, a factor analysis (VARIMAX rotation of the first three principal components) was performed on the correlation matrix of the volumetric contribution of food items for each 5-mm-CL size class of lobsters. Cluster and factor analyses were done with JMP statistical software (SAS Institute, 1995).

Relationships between volumetric contribution and lobster CL were described by least squares linear regression for bivalves, rock crab, and flesh. Relationships between percent occurrence of bivalves and rock crab were described by locally weighted (lowess) regression with a 60% smoothing factor, and by least-squares regression for flesh.

Results

Sample composition, stomach fullness, and types of food items

The 506 lobsters retained for analyses varied in size from 4.3 to 112.4 mm CL (median=35.6 mm CL). Most size classes contained more than 25 lobsters (Table 1). The smallest size class (2.5 to <7.5 mm CL) contained only 16 lobsters with a median of 7.0 mm CL; therefore we refer to this group of lobsters as the 7-mm-CL size class. The 21 lobsters ≥67.5 mm CL were pooled together into a single size class, which we refer to as the 77-mm-CL size class in reflection of their median CL. Females and males accounted respectively for 43.2% and 44.1% of all lobsters examined; the remainder were too small to determine sex. Lobsters were pooled for analyses irrespective of sex because Weiss (1970) and Ennis (1973) concluded that diet was the same for both sexes.

Only two lobsters had empty stomachs and they belonged to the 10-mm size class. With these two empty stomachs excluded, there was a highly significant relationship between the dry mass of stomach contents and lobster CL (Fig. 1). Identifiable food items included macroalgae or benthos that were grouped into broad taxonomic or ecological categories (Table 2). No planktonic organisms were identified from the stomachs, even of the smallest lobsters. However, the crustacean meiofauna group included the remains of very small crustaceans, some like the harpacticoids and ostracods, known to be bottom-dwelling, whereas unidentified minute crustacean remains may have originated from holo- or mero-planktonic forms or from juvenile amphipods, isopods, or carideans. Sand, silt, and infrequently bits of nylon rope were also found in the stomachs. "Flesh" refers to tissue bolus composed of animal soft parts that could not be attributed to a taxon, generally because no distinctive part was found in the stomach along with the tissue or less commonly because distinctive parts from several prey types were present in the stomach but none was attached to the tissue.

Table 1

Number of lobster stomachs sampled by classes of cephalothorax length (CL, in mm). Size classes represent 5-mm groupings except the smallest (7 mm CL) and largest (77 mm CL), which include all lobsters <7.5 mm CL and all lobsters ≥67.5 mm CL, respectively.

Cephalothorax length (size classes)	Number of stomachs		
	1996	1997	Total
7	1	15	16
10	17	20	37
15	28		28
20	38		38
25	56		56
30	45		45
35	52		52
40	51		51
45	45		45
50	45		45
55	31		31
60	25		25
65	16		16
77	21		21
Total	471	35	506

Ontogenetic shifts in diet

A cluster analysis on the volumetric contribution of food items to lobsters by size class yielded four groups: 7 mm, 10–20 mm, 25–60 mm, and 65–77 mm CL lobsters (Fig. 2). These same groups could be seen on a plot of the first three factors of a factor analysis of the correlation matrix of the volumetric contribution of food items (Fig. 3). The three factors explained 68.8% of the variance (39.9%, 18.2%, and 10.7% for factors 1, 2, and 3). The first factor had strong loadings for crustacean meiofauna (0.96), foraminiferans (0.96), bivalves (0.84), macroalgae (0.82), amphipods (0.78), and rock crab (–0.71). Because lobsters in the 7-mm-CL size class had little rock crab in their stomachs, but relatively high proportions of the other food items, they stood out with a very large score (3.1) on this factor. The next two size classes, 10 and 15 mm CL, scored 0.8 and 0.6, respectively. All other size classes scored between 0 and –0.6 on the first factor. The second factor had strong loadings for flesh (0.73), lobster (–0.82), and barnacles (–0.73). Lobsters of the two largest size classes (65 and 77 mm CL) had strong negative scores on this factor (–2.5 and –1.5, respectively), whereas lobsters of the 10–35 mm size classes scored between 0.5 and 1.1. The smallest size class (7 mm CL) and size classes of 40–60 mm CL had scores close to 0. Finally, the third factor had a high loading for carideans (0.74) and somewhat smaller loadings for isopods (0.67), coralline algae (–0.57), and pagurids (–0.54). This third factor separated

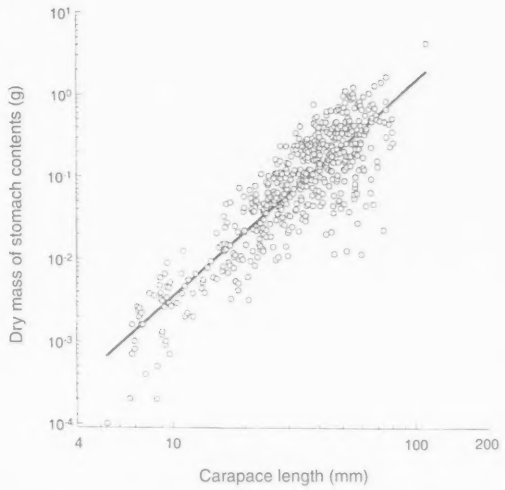

Figure 1

Relationship of dry mass of stomach contents (DM) to cephalothorax length (CL) of lobsters from the Magdalen Islands. Two lobsters of the 10-mm class had an empty stomach and are not shown. Model II regression: $DM = 7.967 \times 10^{-6} \times CL^{2.628}$ [r^2=0.51, P<0.001].

the 25- and 35-mm-CL size classes from the 10–20 mm CL size classes.

For each grouping, Figure 4 shows the specific abundance of each food item plotted against its percent occurrence. Bivalves and flesh accounted for a large proportion of stomach contents of the smallest lobsters (7-mm-CL size class) and were found in ≥75% of stomachs, making them the most important food items for this grouping. Rock crabs, amphipods, and polychaetes contributed 0.2 to 0.4 of stomach volume when they were ingested, but were found in fewer than 30% of the stomachs. Macroalgae and gastropods, on the other hand, were eaten by >50% of small lobsters but were ingested in small volumes. All other prey categories contributed little to stomach volume and were found in a small proportion of stomachs.

Flesh and bivalves were also the most important food items for the 10–20 mm CL lobster grouping (Fig. 4). They accounted for 0.46 and 0.22 of stomach volume, respectively, when they were ingested, and were found in 90% of stomachs. Rock crab was another important prey, with a specific abundance of 0.32 and an occurrence of 41%. Pagurids, carideans, and echinoderms had high specific abundances but were found in less than 5% of stomachs. Gastropods and polychaetes were found in about 40% of stomachs, but accounted for a small fraction of stomach volume. All other prey categories constituted a small fraction of the volume of very few stomachs.

The two main food items of lobsters measuring 25–60 mm CL were rock crab and flesh: specific abundance was high (0.34 and 0.38, respectively) and these food items

Table 2

Major categories of food items, divided into specific food items when possible, and their overall volumetric contribution (total=1) to stomach contents of all examined lobsters from Baie de Plaisance, Magdalen Islands. Abbreviations for major categories of food items are shown in brackets.

Categories of food items	Volumetric contribution
Formaniferans [For]	0.0031
Macroalgae [Alg]	0.0394
Coralline algae (*Corallina officinalis*) [Cor]	0.0178
Hydrozoans [Hyd]	0.0207
Bivalves [Biv]	0.1657
Mytilus edulis	0.0202
Modiolus modiolus	0.0992
Unidentified Pelecypoda	0.0463
Gastropods [Gas]	0.0585
Lacuna vincta	0.0028
Unidentified Gastropoda	0.0057
Polychaetes [Pol]	0.0597
Nereidae	0.0318
Polynoidae	0.0271
Unidentified Polychaeta	0.0008
Barnacles (*Balanus* sp.) [Bar]	0.0012
Crustacean meiofauna [Cru]	0.0053
Harpacticoida	0.0003
Ostracoda	0.0021
Unidentified minute Crustacea	0.0029
Amphipods [Amp]	0.0054
Corophium sp.	0.0004
Gammarus sp.	0.0003
Caprellidea	0.0004
Gammaridae	0.0016
Unidentified amphipods	0.0027
Isopods [Iso]	0.0067
Idotea sp.	0.0013
Idoteidae	0.0019
Unidentified valviferan isopods	0.0034
Carideans [Car]	0.0024
Crangon septemspinosa	0.0010
Unidentified carideans	0.0013
Pagurids [Pag]	0.0416
Pagurus acadianus	0.0051
Paguridae	0.0365
Rock crab (*Cancer irroratus*) [Cra]	0.2637
American lobster (*Homarus americanus*) [Lob]	0.0076
Echinoderms [Ech]	0.0222
Strongylocentrotus droebachiensis	0.0102
Ophiuroidea	0.0012
Unidentified echinoderms	0.0109
Fish [Fis]	0.0066
Flesh [Fle]	0.2724

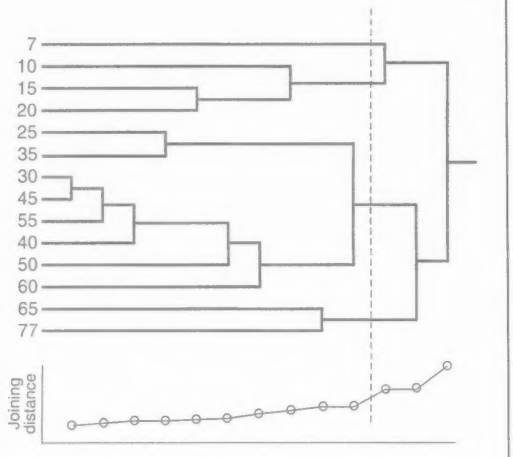

Figure 2

Dendrogram resulting from a cluster analysis on the mean volumetric contribution of major food categories by size class of lobsters from the Magdalen Islands. The bottom graph shows the joining distance at each step. The vertical dashed line indicates the cut-off value for clusters, selected because of the sudden increase in joining distance.

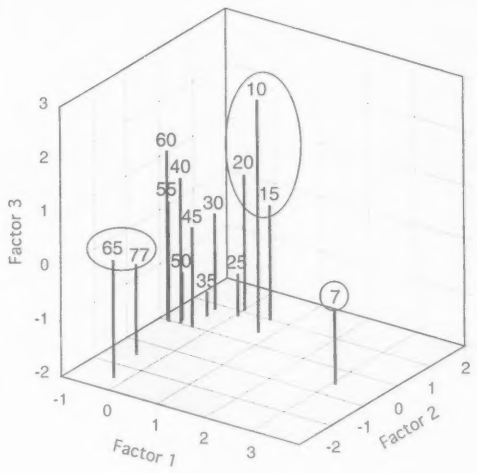

Figure 3

Results of the factor analysis on the correlation matrix of volumetric contribution of major food categories by size class of lobsters from the Magdalen Islands. See text for factor loadings. Three clusters identified in Figure 2 are shown inside ellipses; the other size classes constitute the fourth cluster.

were found in more than 70% of stomachs (Fig. 4). Bivalves were still found in a large proportion of stomachs (87%) but accounted for a low proportion (0.18) of volume. Gastropods, polychaetes, and macroalgae also occurred frequently but accounted for only a small fraction of stomach volume. Pagurids and lobsters were found in few stomachs but contributed >0.2 of stomach volume.

The grouping of the largest lobsters, 65–77 mm CL, had rock crab as the most important food item (specific abundance=0.55; occurrence=86%). Lobsters, pagurids and fish contributed a large proportion of stomach volume when they were eaten, but these prey were ingested by <20% of lobsters. Gastropods, flesh, bivalves, polychaetes, and macroalgae were found in a large proportion of stomachs but occupied a small proportion of the volume of these stomachs.

Overall, bivalves, rock crab, and flesh were the only food items that each accounted for >0.1 of stomach volume for the whole sample (Table 2). For these food items, a significant linear relationship existed between volumetric contribution and lobster CL, the latter explaining 68% to 92% of the variability in volume (Fig. 5). Regression of volumetric contribution on lobster CL produced a negative slope for bivalves and flesh, and a positive slope for rock crab. Similarly, strong linear or nonlinear relationships existed between percent occurrence of these three food items and lobster CL (Fig. 5). Furthermore, large lobsters tended to eat larger rock crabs than small lobsters, as evidenced by the significant positive linear relationship between the CW of rock crabs found in lobster stomachs and lobster CL (Fig. 6).

Discussion

Data

Stomach content analysis is a useful method for the investigation of the natural diet of animals, even though the lack of distinctive hard parts in some prey and differential digestibility of soft and hard body parts limits the spectrum of food items that can be recognized and can lead to biased perception of the relative importance of the food items. We took care to process lobsters as quickly as possible after collection, thus attenuating the effects of differential digestibility, and we examined only intermolt and nonovigerous lobsters, thus reducing sources of diet variability associated with molt cycle and female reproductive status (e.g. Weiss, 1970; Ennis, 1973). In addition, our study was conducted over a small area where the various lobster size classes were evenly distributed; therefore all lobsters potentially could access the same food. We recognize that our volumetric contribution index underestimates the importance of predominant food items, owing to correction for stomachs with multiple food items and total scores >10. However, this was a minor problem because analyses using uncorrected values revealed that the volumetric contribution of the three main food items was underestimated by no more than 2–5% and that relationships to lobster size class were unchanged. Therefore, we are confident that the dietary differences among the lobster size classes that we detected are real and that they

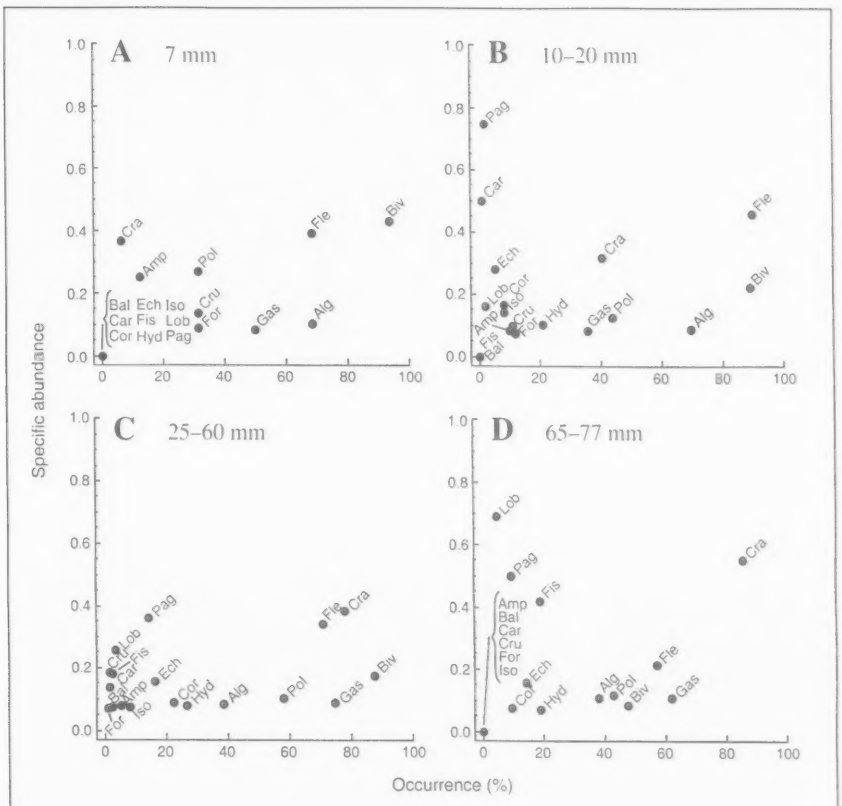

Figure 4

Relationship between specific abundance and percent occurrence for the major food categories in relation to clusters for size classes of the (**A**) 7 mm, (**B**) 10–20 mm, (**C**) 25–60 mm, and (**D**) 65–77 mm CL (see Fig. 2) for lobsters from the Magdalen Islands. Refer to Table 2 for abbreviations of major food categories.

reflect mainly changing lobster preferences and differential accessibility of prey types.

Ontogenetic shifts in diet

There was clear evidence of a progressive dietary shift with increasing lobster size at our study site. Smaller lobsters relied to a greater extent than larger lobsters on soft or easily acquired food items (flesh, sessile juvenile bivalves, macroalgae, meiobenthic crustaceans, and foraminiferans). Larger lobsters fed on bigger, more mobile and also more nutritious prey, including crustaceans that were protected by heavy shells, and fish. Fishes were probably taken by predation (see Weiss, 1970) because there was no fishing activity at or near our study site that might have provided lobsters with fish bait or discards.

The most striking ontogenetic changes in volumetric contribution of prey types occurred for rock crab and bivalves, the former increasing from 0.07 to 0.53 and the latter decreasing from 0.28 to 0.02 from the smallest to the largest lobster size class, respectively (Fig. 5). Only limited comparisons with other studies are possible, given the differences in methods and in the size range of lobsters examined. However, the observed trends of increasing importance of rock crab and of decreasing importance of bivalves with increasing lobster size were consistent with the analyses of Scarratt (1980) and of Carter and Steele (1982b), and they suggest that lobsters are not simply opportunistic or unspecialized feeders (see Elner and Campbell, 1987).

Multivariate analysis of lobster diet resulted in size groupings that are quite consistent with Lawton and Lavalli's (1995) size classification of the early life-history phases based on a broad set of behavioral and ecological criteria. Major shifts in diet in the present study occurred at about 7.5, 22.5, and 62.5 mm CL (Fig. 2). The two classifications differ in the smaller size for the transition from the first to second group (7.5 mm in our diet-based classification compared with 14.5 mm CL in Lawton and Lavalli's scheme), but the size for transition from the second to the

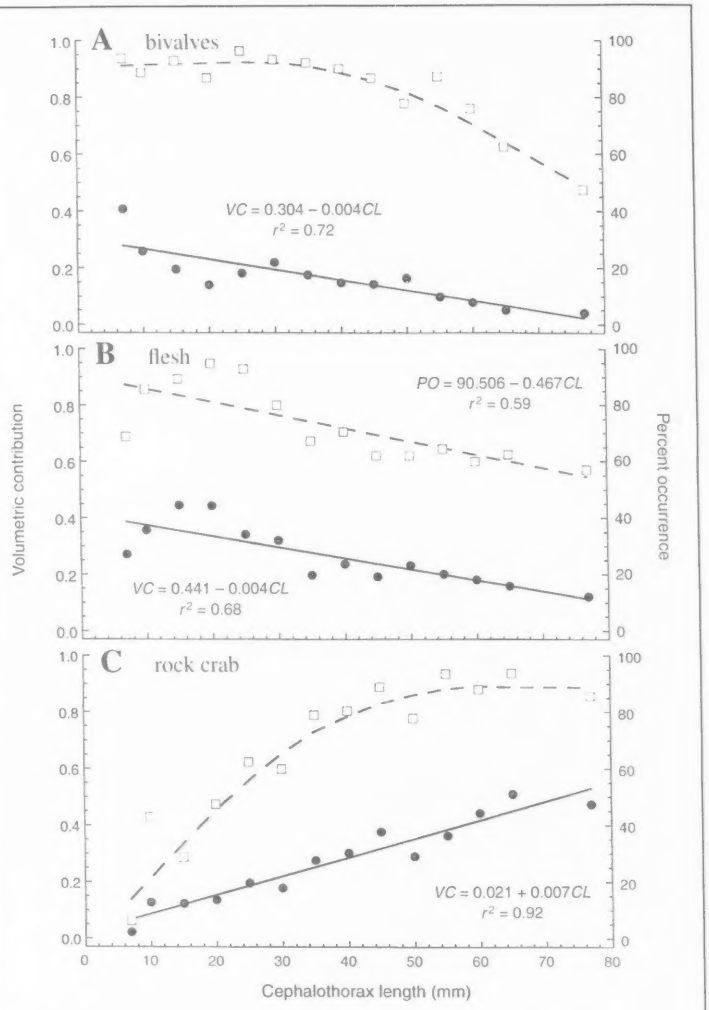

Figure 5

Relation between percent occurrence (PO, □) or volumetric contribution (VC, •) and lobster cephalothorax length for the three main food items of lobsters from Magdalen Islands: (**A**) bivalves, (**B**) flesh bolus, and (**C**) rock crab. All linear regressions are highly significant (P<0.001).

third group is the same in both studies (22.5 and ~25.0 mm CL). Comparison of the size threshold for transition from the third to the fourth group is less appropriate because Lawton and Lavalli (1995) considered this threshold to be determined by physiological maturity, which is a temperature-dependent trait that varies among regions.

Natural diet of shelter-restricted juveniles

This first investigation of the diet of SRJ lobsters does not support the view that these juveniles derive a substantial portion of their diet by suspension feeding and browsing in their shelters, at least at our study site and during the two years we sampled. With respect to suspension feeding, there was no evidence of planktonic organisms in stomachs, although some of the unidentified prey of the crustacean meiofauna category may have been planktonic. Foraminiferans, harpacticoids, ostracods, and macroalgal debris represented food items that potentially could be browsed within shelters. However, these taxa together contributed relatively little to stomach volume of lobsters in the 7-mm size class (0.14 for the combined categories,

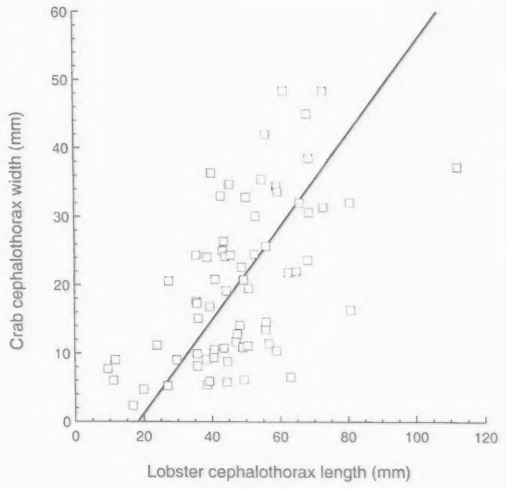

Figure 6

Relationship of predator (lobster) size to prey (rock crab) size, based on rock crab cephalothorax width (CW) estimated from measurements of indicator fragments and lobster cephalothorax length (CL), for the Magdalen Islands. Model II regression: $CW = -12.341 + 0.677CL$ [r^2=0.34, P<0.001].

in spite of the fact that one or the other category occurred in 88% of stomachs) and even less to stomach volume of lobsters in the 10-mm size class (0.10, 86%). During our study, lobsters settled in August at sizes of 4.3–5.2 mm CL and grew to 12–14.5 mm CL by October (Sainte-Marie et al., 2001). Thus, we sampled the lobster population during the only period of time when SRJs were present and seasonal sampling bias cannot be invoked to explain the lack of plankton in their diet.

The other food items in the stomachs of SRJs, and especially the predominant bivalves and flesh (Figs. 4 and 5), probably were derived by predation and scavenging. Bivalves in the stomachs of SRJ lobsters were represented by recently settled *Modiolus* and *Mytilus*. Mussel spat may settle aggregatively and quite synchronously, forming dense patches that can provide a short-term prey pool requiring little or no search time (e.g. Auster, 1988). Furthermore, because mussel spat often settle in crevices or under rocks (e.g. Nair et al., 1975), SRJs could access them with little or no risk of exposure to predators. Lawton (1987) argued that dominance and territoriality were likely to exist early in the ontogeny of lobsters, as demonstrated subsequently (James-Pirri and Cobb, 1999; Paille and Sainte-Marie, 2001), and that prolonged occupation and defense of shelters located close to a food patch would be advantageous for juveniles. Exploitation of mussel patches, inferred from the present study, is consistent with that hypothesis.

Flesh (tissue boluses) that could not be attributed to a particular animal for lack of indicator fragments was a very important food item in the diet of SRJs, both in terms of percent occurrence and of volumetric contribution (Figs. 4 and 5). Elner and Campbell (1987) also found that unidentified animal tissue was one of the most frequent and most volumetrically important foods in the stomachs, however, of larger lobsters. Weiss (1970) observed that adolescent and adult lobsters often captured crabs or other shelled prey, cracked them open, and then selectively ingested only soft tissue. Interestingly, the percent occurrence and volumetric contribution of flesh to diet was greater in lobsters of size classes ≤30 mm CL (i.e. SRJs and emergent juveniles) than in larger lobsters (Fig. 2). It is unlikely that the smallest of lobsters could find (within the confines of their shelter) and subdue prey sufficiently large to provide tissue boluses devoid of hard parts. Furthermore, claws are not differentiated into cutter and crusher forms in SRJs (Govind and Lang, 1978; Costello and Govind, 1984) and early juveniles may be incapable of breaking open shelled prey (Costello and Lang, 1979; Lawton and Lavalli, 1995). Therefore, flesh ingested by SRJs and emergent juveniles probably was obtained by scavenging animal remains. Considering that larger lobsters may hoard and bury food in or nearby their dens (Herrick, 1895; Smith, 1976; Lawton, 1987; Wickins et al., 1996), we propose that early juveniles exploit the meal scraps or food reserves of larger lobsters. Indeed, we observed that small lobsters often occupied galeries beneath, or in rock pilings nearby, the dens of larger lobsters. This is consistent with reports that odor from conspecific adults is a proximate cue for lobster settlement (Boudreau et al., 1993). Cohabitation of small lobsters with large lobsters would offer the former protection from predators and a potentially abundant, high-quality, sheltered food source, and would therefore represent a form of commensalism. The risk of cannibalism for small lobsters living in the vicinity of larger lobsters probably does not offset the benefits. Few lobster remains were found in lobster stomachs in this (Fig. 4) as in other studies (Weiss, 1970; Carter and Steele, 1982b; Elner and Campbell, 1987), and an unknown proportion of those remains may have been exuviae.

Some other rarer food items found in the stomachs of SRJ lobsters were probably taken by predation, possibly within, but more likely in the neighborhood of, the lobsters' shelters. The most important of these prey by volumetric contribution were polychaetes, comprising juvenile nereids and polynoids that are frequently found in soft sediment or on the underside of rocks, and recently settled rock crab. Similarly, amphipods and gastropods found in the stomachs of SRJs were juveniles or small species that may abound in crevices and in spaces beneath rocks.

A carnivorous, high-energy diet such as the one demonstrated for SRJs in our study would promote growth from settlement time. By contrast, Lavalli (1991) demonstrated that a diet of only diatomous algae was insufficient for extended growth and survival of early juvenile lobster. A diet of mesozooplankton sustained growth of juvenile lobsters, at least for some time after settlement (e.g. Daniel et al., 1985; Barshaw, 1989; Lavalli, 1991). However, Lawton and Lavalli (1995) pointed out that intermolt periods tended to be longer and molt increments smaller in laboratory-held,

juvenile lobsters reared on mesozooplankton than in wild lobsters, suggesting that the latter incorporated more nutritious foods into their diet.

The finding that early juvenile lobsters are primarily predators or scavengers, if confirmed by studies at other sites, has implications for the development and implementation of artificial reefs. Such structures are increasingly being considered as a means to enhance lobster productivity on traditional grounds or to expand lobster habitat onto less hospitable grounds (e.g. Gendron, 1998). The carnivorous benthic feeding mode of SRJs and of emergent juveniles at our site implies that successful reefs will have to be designed, localized, and weathered so that they are initially well colonized and subsequently regularly colonized by benthic prey that are easily accessible and of high nutritional value to juvenile lobsters. Additionally, if SRJs and emergent juveniles derive some protective and nutritional benefits from the presence of larger conspecifics, reefs designed to offer shelter to a full suite of lobster sizes may prove to be more productive in the long term than reefs offering shelter only to small lobsters.

Importance of rock crab to lobster

Several previous studies have noted the importance of rock crab in the diet of lobster (Reddin, 1973; Evans and Mann, 1977; Carter and Steele, 1982a). Boghen et al. (1982) found that juvenile lobsters survived and grew better on a diet containing crab protein alone than on a diet of live brine shrimp (*Artemia salina*) or of protein extracts from urchin (*Strongylocentrotus droebachiensis*), mussel (*Mytilus edulis*), or shrimp (*Penaeus* sp.). Gendron et al. (2001) found that condition, somatic growth, and gonadal development of lobster increased with increasing amount of rock crab in diet. In nature, even SRJs may benefit from a diet including large amounts of rock crab protein because they preyed directly on very small rock crabs (Figs. 4 and 5), and the tissue boluses they contained may have been that of rock crab (see above).

We were able to establish a positive size relationship for lobster preying on rock crab (Fig. 6). The smallest rock crab prey were 2–6 mm CW and belonged to the first benthic instars of this species. In our study, apparently no rock crabs larger than 50 mm CW were consumed by lobsters, and the maximum ratio of crab CW over lobster CL was 0.90, even though rock crabs up to 120 mm CW were seen (own personal diving observations). In the laboratory, Weiss (1970) observed that lobsters of 60–80 mm CL attacked crabs offered in the size range of 62–78 mm CW. Lawton and Lavalli (1995) reported that juvenile lobsters can subdue juvenile intermolt rock crabs up to approximately 0.40 times their own body size. Their observation was based on the comparison of predator and prey wet masses; when expressed in terms of crab CW over lobster CL, the maximum ratio was equivalent to about 1.27.[1] This ratio of prey CW to predator CL is somewhat larger than that derived from our stomach analyses. Because lobsters probably ingest only soft tissue when the prey-predator size ratio is sufficiently high (Weiss, 1970; and see above), our analysis of rock crab prey-size frequencies may correctly estimate the minimum prey size but underestimate the maximum prey size and the volumetric contribution and occurrence of rock crab in the diet of any given lobster size class. Nevertheless, the present study clearly shows that all lobster size classes rely on rock crab as food and that the size spectrum of rock crab that is used by lobsters is broad and includes even those at the settlement stage. Given the much greater economic value of lobster in relation to rock crab, and the trophic dependency of the former on the latter, caution should be exercised in developing rock crab fisheries (Gendron and Fradette, 1995).

[1] Lawton, P. 2000. Personal commun. Fisheries and Oceans Canada, St. Andrews, New Brunswick, Canada.

Acknowledgments

We thank our diving partners F. Hazel, J.-G. Rondeau, J. A. Gagné, K. Gravel, R. Larocque, J.-F. Lussier, N. Paille, and A. Rondeau. We are particularly grateful to J. Hudon for her major contribution to the identification of stomach contents and to three anonymous reviewers for constructive comments. This is a contribution to the Canadian Atlantic-Wide Lobster Studies (CLAWS) research initiative of Fisheries and Oceans Canada.

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Abstract–Skeletochronological data on growth changes in humerus diameter were used to estimate the age of Hawaiian green seaturtles ranging from 28.7 to 96.0 cm straight carapace length. Two age estimation methods, correction factor and spline integration, were compared, giving age estimates ranging from 4.1 to 34.6 and from 3.3 to 49.4 yr, respectively, for the sample data. Mean growth rates of Hawaiian green seaturtles are 4–5 cm/yr in early juveniles, decline to a relatively constant rate of about 2 cm/yr by age 10 yr, then decline again to less than 1 cm/yr as turtles near age 30 yr. On average, age estimates from the two techniques differed by just a few years for juvenile turtles, but by wider margins for mature turtles. The spline-integration method models the curvilinear relationship between humerus diameter and the width of periosteal growth increments within the humerus, and offers several advantages over the correction-factor approach.

Age and growth of Hawaiian green seaturtles (*Chelonia mydas*): an analysis based on skeletochronology

George R. Zug

Division of Amphibians and Reptiles
Department of Systematic Biology
National Museum of Natural History
Washington, D.C. 20560-0162
E-mail address: zug.george@nmnh.si.edu

George H. Balazs
Jerry A. Wetherall

Honolulu Laboratory
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2570 Dole St., Honolulu Hawaii 96822-2396

Denise M. Parker
Shawn K. K. Murakawa

Joint Institute for Marine and Atmospheric Research
2570 Dole St.
Honolulu, Hawaii 96822-2396

The Hawaiian population of the green seaturtle (*Chelonia mydas*) provided some of the first published growth data (Balazs, 1979, 1980, 1982) for this species. These early data showed how slowly seaturtles grow and how long a female must survive simply to lay her first clutch of eggs. Twenty or more years to reach sexual maturity seemed biologically unrealistic, yet slow growth and late maturity has been repeatedly confirmed for some seaturtle species, e.g. Bahamian *C. mydas* (Bolten et al., 1992), West Atlantic *Caretta caretta* (Parham and Zug, 1998). Slow growth and the resulting delayed maturity greatly affect the demography of a population (Crouse et al., 1987; Chaloupka and Musick, 1996). An understanding of growth and growth-pattern variation in seaturtles is an important prerequisite to the development of population models that are required to guide seaturtle population recovery and conservation.

Green seaturtles within the Hawaiian Islands contribute to the larger Indo-Pacific *C. mydas* gene pool, yet the nesting females of the Hawaiian population comprise a distinct genetic unit and contain a unique mtDNA haplotype (Bowen et al., 1992). Except during their posthatching pelagic phase, the great majority of Hawaiian green seaturtles reside in coastal waters, primarily around Hawaii, Kauai, Maui, Molokai, Oahu, and other islands in the southeastern part of the Hawaiian chain. Most reproduction takes place at French Frigate Shoals in the Northwestern Hawaiian Islands (Balazs, 1980; Wetherall et al., 1999). The population of Hawaiian *Chelonia mydas* has benefited from over two decades of intense conservation management (Balazs, 1998). Despite important early research on the Hawaiian population of *C. mydas* (Balazs, 1982), the patterns of growth within and among the geographic habitat components of this population have remained incompletely documented (Balazs et al., 1994, 2000). The chief reason for this has been a lack of methods to age sea turtles. This deficiency has been overcome recently by the development of skeletochronological techniques that estimate age from the number of growth increments formed on the humerus (Parham and Zug, 1998).

Manuscript accepted 20 August 2001.
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Our goal in this study was twofold. First, we used humerus growth-increment data to estimate ages of a sample of Hawaiian green seaturtles from various locations in the archipelago and developed a growth model for the general Hawaiian population; geographic variation in growth will be addressed in a subsequent paper. Second, we compared two different methods of deriving the age estimates, the so-called "correction-factor" method described by Parham and Zug (1998) and a newer approach, the "spline-integration" method, introduced in the present study.

Materials and methods

Our sample consisted of 104 individuals of *C. mydas*, collected from the islands of Hawaii, Kauai, Lanai, Maui, Oahu, and the Northwestern Hawaiian Islands; the Oahu sample predominated with 64 individuals. All individuals were measured to the nearest 0.1 cm straight carapace length (SCL). The smallest individual was a 5.3-cm-SCL hatchling. The smallest posthatchling was a pelagic juvenile (of assumed Hawaiian origin) recovered from the former squid driftnet fishery north of the island chain. All other posthatchling turtles were from coastal Hawaiian waters, found stranded dead and retrieved by the National Marine Fisheries Service's Hawaiian Islands Seaturtle Stranding Network. The salvaged turtles ranged from 28.7 to 96.0 cm SCL. The sample was divided into eight 10-cm size classes; representation was roughly equivalent for the middle six classes (Fig. 1). The 30–39 cm sample contained only turtles in the upper quartile of this size class. Each turtle was necropsied and its right humerus removed for skeletochronological examination. The necropsy data included a complete set of carapace measurements, organ condition evaluations, and information on fibropapilloma tumor occurrence and severity; see Work and Balazs (1999a, 1999b) for details on the entire data set. In addition to the skeletochronological data, we used only the SCL measurements and tumor-evaluation observations in the present study.

Where possible, we selected tumor-free individuals for the present analysis because our goal was to examine the overall growth pattern for normal Hawaiian *Chelonia mydas*. Because the prevalence of fibropapillomatosis is high in the wild Hawaiian population (Murakawa et al., 2000), we included in our sample individuals with fibropapillomas. but otherwise appearing normal, in order to ensure adequate representation in the larger size classes. Healthy animals were those showing no evidence of weight loss or other indicators of illness and no evidence of disruption or retardation of normal growth. Individuals with tumors represented 27% of the 50–59 cm, 50% of 60–69 cm, 76% of 70–79 cm, 73% of 80–89 cm, and 17% of 90–99 cm SCL size classes (Fig. 1).

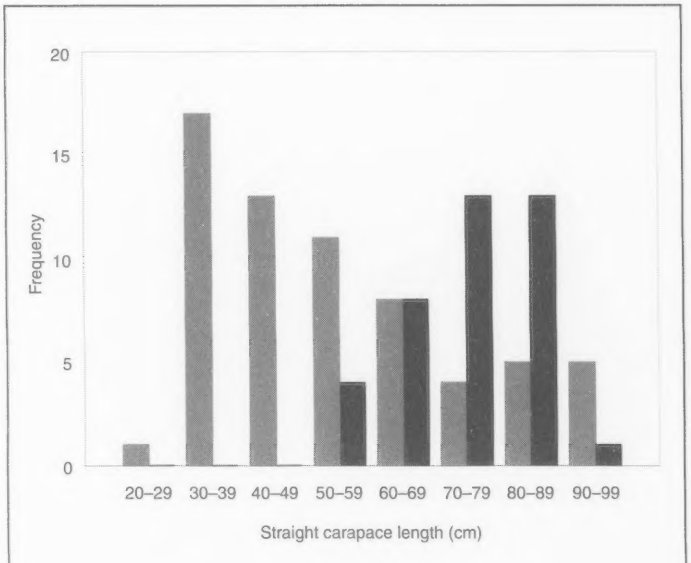

Figure 1

Size (straight carapace length) distribution of the Hawaiian *Chelonia mydas* skeletochronological sample. The members of each class are segregated into individuals without (shaded bar) and with (black bar) fibropapilloma tumors. Tumors in our sample are present only in larger turtles.

Our skeletochronological data derived from cross-sections (0.6–0.8 mm thick) from the middle of the humeral shaft just distal to the deltopectoral crest and at the narrowest diameter of the diaphysis (Zug et al., 1986). On each specimen, we counted the number of visible growth layers and measured the widths (long-axis diameters) of the humerus at each successive growth cycle and the width of the resorption core. Bone sections were taken from mid-shaft, the narrowest location of the bone, because the humerus retains the greatest number of periosteal growth layers there, and hence this location permits the most accurate estimation of the number of growth cycles (periosteal layers) and the relative rates of growth (=successive humerus diameters).

We used two procedures for estimating the total number of growth layers, and hence age, of each turtle. In the correction-factor (CF) method, as described in Parham and Zug (1998), the turtle's age is estimated as the number of growth layers observed in the outer region of the humerus section plus the predicted number of resorbed growth layers represented in the remodeled core of the humerus. The latter, unobservable component is estimated as $C\,(R - R_H)$, where R is the radius of the absorption core, R_H is the radius of a hatchling's humerus (before the beginning of increment formation), and C is the so-called correction factor. The correction factor is a constant "aging rate" (yr/mm) assumed to apply to the resorption core, and calculated as the reciprocal of the mean growth layer width in small turtles. The mean growth layer width was estimated from 129 periosteal growth layer widths observed in 34 turtles

with SCLs <60 cm and resorption core diameters <19.0 mm. Selecting only small turtles with minimum core diameters reduces the frequency of the narrower periosteal layers found in the outer margin of the humerus in larger turtles; hence, it reduces the possibility of overestimating the number of layers in the resorption core. The resulting correction factor was used to estimate the number of resorbed periosteal layers.

A second method, spline integration (SI), is introduced here. The SI method uses a scatterplot smoothing spline (Härdle, 1990; Hastie and Tibshirani, 1990) to model the relationship between the aging rate and humerus diameter. Once the aging function is estimated, a turtle's age is estimated by integrating the spline over the total diameter of the turtle's humerus section. The method of modeling increment width patterns in hard parts and of estimating age by the integration of the resulting aging function was first formalized by Ralston and Miyamoto (1983) for a Hawaiian snapper and first applied to seaturtles by Zug et al. (1995). In those applications, the aging rate was a parametric function of size. In our analysis, we modeled the aging rate nonparametrically by fitting a smoothing spline to pairs of observations of growth-layer width and humerus diameter. The SI approach uses the same source of data as the CF method but without selection. Lines of arrested growth (LAG) delimit each observable growth layer. Increment width is measured as the difference between the humerus diameters at the outer LAG and the inner LAG. Assuming an increment represents one year of growth, each increment width measurement provides a measure of the humerus growth rate (mm/yr) and its reciprocal, a measure of the aging rate (yr/mm) at the observed humerus diameter (the mean diameter of the pair of LAGs). The skeletochronological sample yielded 269 such observations of aging rate and humerus diameter. The aging rates were grouped in 1-mm intervals of humerus diameter and averaged. A cubic smoothing spline was fitted to the mean aging rates by using S-PLUS (MathSoft, Inc., 1999). The age (yr) of each turtle was estimated by integrating the aging spline from its origin to the observed outside diameter of the humerus section.

To assess the effect of estimation method on age estimates, the data were divided into 10-cm SCL groups. Within each group a Student's t statistic was used to test the hypothesis that the two methods give equal age estimates.

Nonparametric growth models were estimated based on the CF- and SI-derived age estimates and associated carapace lengths, by using the same S-PLUS procedure employed for the SI-method aging spline. The validity of the growth models was judged qualitatively by comparing growth predicted by the models with observed growth in a sample of 171 Hawaiian green turtles tagged and recaptured in waters around Molokai (Balazs et al., 1999).

To assess uncertainty in the SI-based growth curve, the 269 pairs of aging rate and mean humerus diameter data were resampled 100 times, and the SI procedure applied to each bootstrap replicate data set. The 100 aging curves derived in this manner generated a bootstrap distribution of estimated age for each turtle. Nonparametric growth curves were then fitted to each derived data set, producing bootstrap distributions of predicted mean length at age. Empirical confidence intervals for the predicted mean length at age were approximated by using percentiles of the latter bootstrap distributions.

A linear regression of SCL on outside humerus diameter was estimated for the 104 sample turtles. The slope of the linear predictor was applied to the 269 humeral increments to estimate a corresponding set of carapace increments, presumed to represent annual growth. These growth rate estimates were summarized in box plots over 10-cm intervals of SCL. Mean growth rate as a function of estimated age was also estimated by computing finite differences of the SI-based growth model.

Results

Patterns in humerus growth and aging

Carapace length has a strong linear association with humerus diameter (Y=0.643 + 2.326X [where Y=SCL cm; X=humerus diameter mm], r^2=0.98, P<0.001, n=104 including the hatchling). Humerus growth-increment width, on the other hand, is nonlinearly associated with humerus diameter at the point of growth (Fig. 2). Specifically, growth increments tend to be larger when the turtles are smaller (i.e. at smaller humerus diameters) and decline as the turtles grow. Variation in humerus increment width (growth rate) shows the same pattern. The estimated aging rate, as the reciprocal of growth rate, increases as the turtles grow. The aging rate does not increase uniformly (Fig. 3). Rather, it increases gradually in small turtles, plateaus over a broad range of length for mid-size turtles, increases abruptly as turtles approach maturity, and maintains an increased rate as the mature turtles grow.

Age and growth-rate estimates

In the CF-method analysis, the correction factor, C, was estimated as 1.14 yr/mm. The resulting age estimates range from 4.1 to 34.6 yr (n=70; excluding the hatchling with age zero). The smallest turtle in the sample had the lowest age estimate and the two largest turtles, the highest estimates. Only 68% could be aged by the CF method. Skeletochronology requires a pattern of distinct layering within the bony element examined. Such patterns are most evident in the smaller, presumably younger, individuals, and the frequency of individuals with distinct periosteal layers decreases as body size increases. In selecting specimens for the CF analysis, growth layers were sufficiently distinct to estimate the number of resorbed layers, and hence the age, in decreasingly fewer turtles: 89% of turtles in the 30–69 cm SCL group, 72% in the 70–79 cm group, 18% in the 80–89 cm group, and 29% in the >89 cm group were used in the CF analysis. Of the individuals for which we were unable to obtain an estimate of resorbed layers, a nearly equal number (48%) had fibropapillomas. The prevalence of tumors for the CF-aged subsample (31%) was somewhat less than in the total sample (37%). Importantly, the tumor prevalence in the subsam-

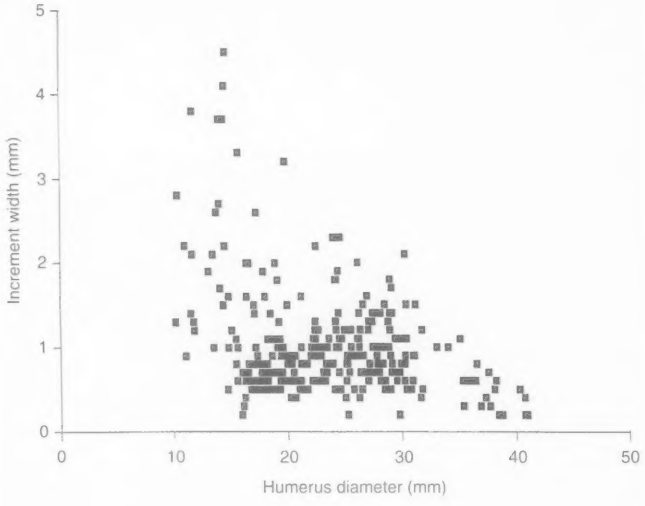

Figure 2

Humerus growth increment width (the increase in humerus diameter) in relation to humerus diameter (mean of the inner and outer diameters). Mean diameter better reflects the size of the humerus during the entire growth interval than does outer diameter.

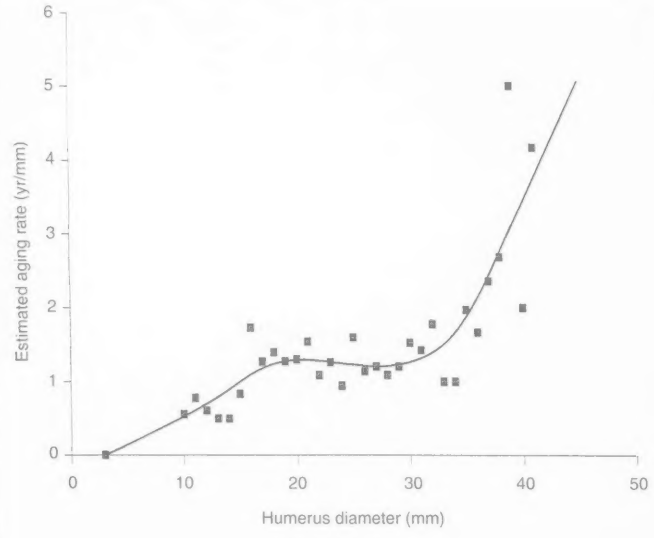

Figure 3

Estimated "aging rate" (average of the reciprocals of the humerus growth-increment widths) in relation to humerus diameter and a fitted smoothing spline. The expected age at a given humerus diameter is obtained by integrating the spline up to the specified diameter. Not all members of the sample could be aged by the CF method; see explanation in "Materials and methods" section.

ple retained for CF analysis and the subsample excluded from analysis were not significantly different (chi-square test of homogeneity χ^2=2.80, 1 df). A nonparametric growth model was estimated by fitting a scatterplot smooth to the carapace length and estimated age data (Fig. 4A). Because the CF method could not be applied to the largest turtles in the sample, the model provided no information about growth in mature turtles.

Age estimates for posthatchling turtles based on the SI method range from 3.3 to 49.4 yr (n=103). The nonparametric growth model for these data fitted very well (Fig. 4B), a result not unexpected given the dependence of the SI age estimate on humerus diameter and the tight linear relationship between humerus diameter and carapace length. Variation in carapace length around the SI growth model reflected only variance in the linear relationship between carapace length and humerus diameter; it did not incorporate variance in the age of turtles at a fixed humerus diameter or estimates of their age. The bootstrap distributions of age estimates for the SI method suggested that age estimates for a turtle can vary by up to 10 years (Fig. 5A). Nevertheless, the nonparametric confidence intervals for predicted mean length at age were narrow (Fig. 5B).

Although the CF and SI methods yielded different estimates of age (Fig. 4), over a wide range of carapace lengths, the differences were not striking. The magnitude and direction of differences in age estimates depend on SCL. Judging from the fitted smooth curves, for turtles up to about 81 cm SCL, the correction factor method was expected to give estimates of age up to 2 years higher than those produced by the spline-integration method. For larger turtles, however, age estimates derived from the correction-factor method were predicted to be as many as 10 years (or more) lower than those generated by spline integration (Fig. 6). The t-tests (Table 1) indicated there were highly significant differences in age estimates between methods within the 40–50 cm size group (t=4.36, 9 df) and the 50–60 cm group (t=4.66, 12 df). Differences for the 30–40 cm, 60–70 cm, and 70–80 cm size groups were nonsignificant; samples were too small for comparisons in other size groups.

The Molokai mark-recapture data allowed a visual comparison of observed growth and growth predicted by the CF and SI models derived from skeletochro-

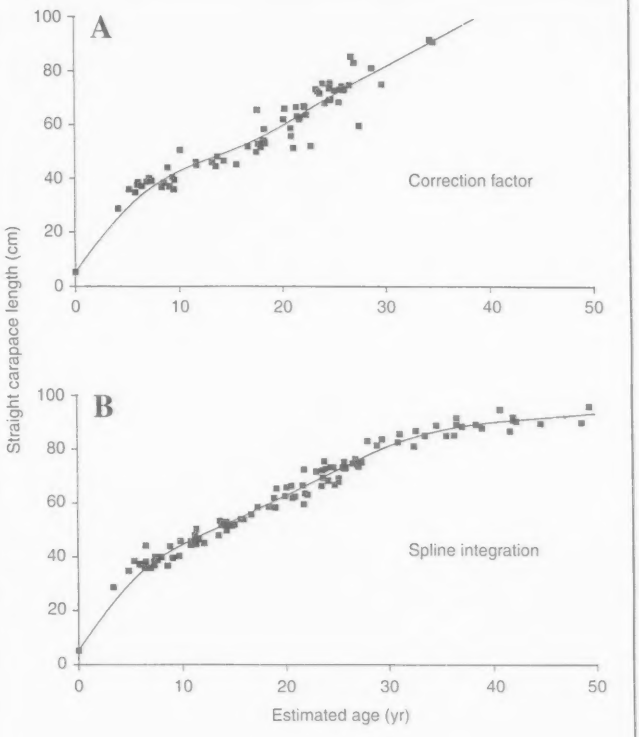

Figure 4

Relationship between observed carapace length and estimated age (squares) for the two methods of age determination: correction factor (**A**) and spline integration (**B**). Fitted growth models (curves) are cubic smoothing splines.

Table 1

Mean age estimation for correction-factor and spline-integration methods for 10-cm length groups. Estimates of mean age vary significantly between estimation methods for turtles in the middle length groups. ** indicates a significant difference.

Length group (SCL, cm)	Sample size	Mean age estimate (yr)		
		Correction-factor method (CF)	Spline-integration method (SI)	t [df], P
30–40	14	7.3	6.9	1.09 [13], 0.296
40–50	10	12.9	11.0	4.36 [9], 0.002**
50–60	13	19.1	15.8	4.66 [12], 0.001**
60–70	14	22.1	22.1	–0.06 [13], 0.952
70–80	13	25.3	25.6	–0.67 [12], 0.514

nological data (Fig. 7). In plotting the growth vectors for marked (tagged) turtles, we fixed the origin of each vector by assuming that the carapace length at time of first capture was given exactly by the CF- or SI-based growth curve. The observed length at recapture and time at liberty then determined the endpoint coordinates of the growth vector. Despite considerable variation in the observed growth of the marked turtles, the growth vectors were generally concordant with the growth model predictions (Fig. 7).

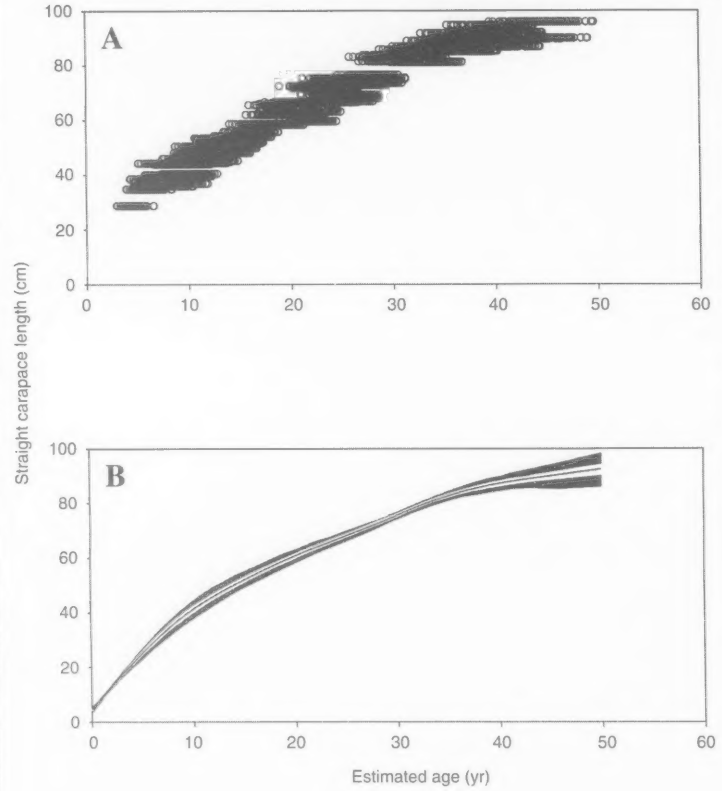

Figure 5

(**A**) Bootstrap distributions of estimated age at observed SCL generated by resampling the data for aging rate to humerus diameter 100 times and by applying the spline-integration method to each bootstrap replicate. (**B**) Corresponding distribution of growth curves, described by the bootstrap mean growth curve (line) and the approximate 50% and 95% confidence intervals for predicted mean length at age (outer and inner edges of solid region).

Age- and length-specific growth rates

The box plots of the SI-estimated carapace growth rates (Fig. 8) indicated relatively fast growth for smaller turtles, a reduced growth rate remaining fairly constant over intermediate length classes, and declining growth rates in larger, mature turtles. Mean carapace growth rate declined from 4.4 cm/yr for turtles in the 20–30 cm SCL group to less than 1 cm/yr for mature turtles in the 90–100 cm group, and remained around 2.0–2.5 cm/yr for immature juveniles in the intermediate length groups (Table 2, Fig. 8). Differences in mean growth rate among the intermediate length groups were not significant. The average growth rates predicted by first differences of the SI-based growth model (Fig. 9) indicated a similar pattern, as expected, showing a decrease in growth rate during the first decade of life (when Hawaiian green turtles are still foraging in the open ocean or in the early years of their residence in inshore habitats), relatively constant growth during the next 15–20 year interval, and a further decline in growth rate as the turtles approach 30 years of age. The growth rate appears to remain low in older turtles.

Discussion

Age and growth-rate estimates

Age estimates by both methods indicate an age range of 4–49 years for the Hawaiian green seaturtles in their coastal habitats. The pelagic juvenile (28.7 cm SCL) in our sample was about four years old (4.1 and 3.3 yr by CF and SI methods, respectively). The smallest juveniles (35–37 cm SCL) in coastal waters were 6 to 9 years old by the CF

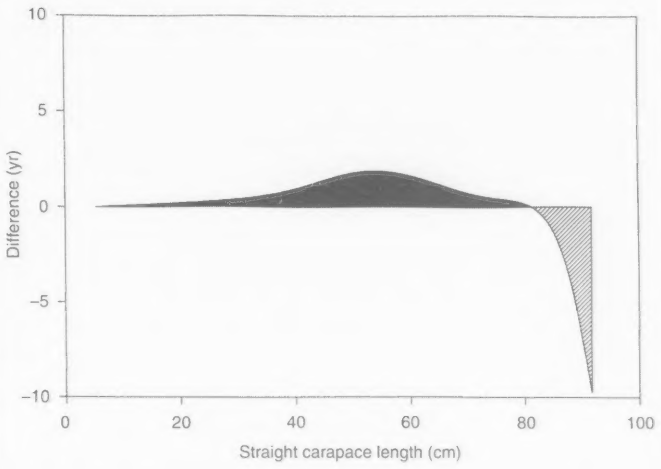

Figure 6

Difference in estimated age (yr) between the correction-factor method and the spline-integration method within the comparable range of carapace lengths (SCL). For positive values (black region), the CF method gives older ages and for negative values (striped region), younger ages.

method and 4 to 10 years old by the SI method. These age estimates for Hawaiian greens in the last years of their pelagic developmental stage are similar to those reported for *C. mydas* populations in the southern Great Barrier Reef (SGBR) (5–6 yr; Chaloupka et al., in press) and for the Atlantic coast of central Florida (3–6 yr; Zug and Glor, 1999). The smallest *C. mydas* turtle in the Florida sample was 28 cm SCL (several others were less than 35 cm), whereas the smallest SGBR turtle was 38.5 cm CCL (Limpus and Chaloupka, 1997) and the smallest Hawaiian specimen was 34.8 cm SCL, indicating an earlier shift from pelagic to benthic life in Florida greens.

The growth of the juvenile turtles predicted by both CF and SI models is consistent with the growth observed in the Molokai mark-recapture sample, but predictions of the CF model depart from the tag-recapture results in older turtles (Fig. 6). Mean growth rates for smaller (30–60 cm) turtles estimated from our transformed humerus increment data (Table 2) were about half as high as growth rates reported for turtles of the same size in most Atlantic and Caribbean locales (based on tagging and skeletochronology: Tables 2 and 3 in Zug and Glor, 1999). Our estimates were similar to the observed growth rates of tagged turtles in Kiholo Bay, Hawai'i (Balazs et al., 2000) and nearly twice as high as rates observed in some other Pacific samples (Galápagos, Heron Island; Tables 2 and 3 in Zug and Glor, 1999). Subsequent studies of Australian populations (Limpus and Chaloupka, 1997; Chaloupka et. al., in press) have shown a mid-juvenile growth rate more similar to our estimates; however, growth rate is associated with a growth surge in the Australian turtles over a narrow mid-juvenile length range (50–60 cm SCL). Such a spurt in growth was not evident in our SI-based growth curve, and growth rates were fairly constant in the 40–80 cm size classes (Fig. 8).

Table 2

Growth rate statistics by length class. Rates were derived from spline-integration data.

Length group (SCL, cm)	Growth rate (cm/yr)		
	Sample size	Mean	SD
20–30	9	4.4	2.2
30–40	37	3.5	2.7
40–50	67	2.1	1.2
50–60	53	2.3	1.0
60–70	62	2.2	0.9
70–80	21	2.1	1.0
80–90	12	1.3	0.5
90–100	7	0.6	0.3

Our age and growth estimates pertain to the Hawaiian population as a whole, because the sampled turtles originated from locations throughout the archipelago. Some variation in age and growth between island foraging groups is likely, given the extensive latitudinal range of the habitats and the associated variation in physical and biological parameters affecting growth (Balazs, 1982). A geographic analysis of age and growth will be the subject of a future study. Future study will also investigate the

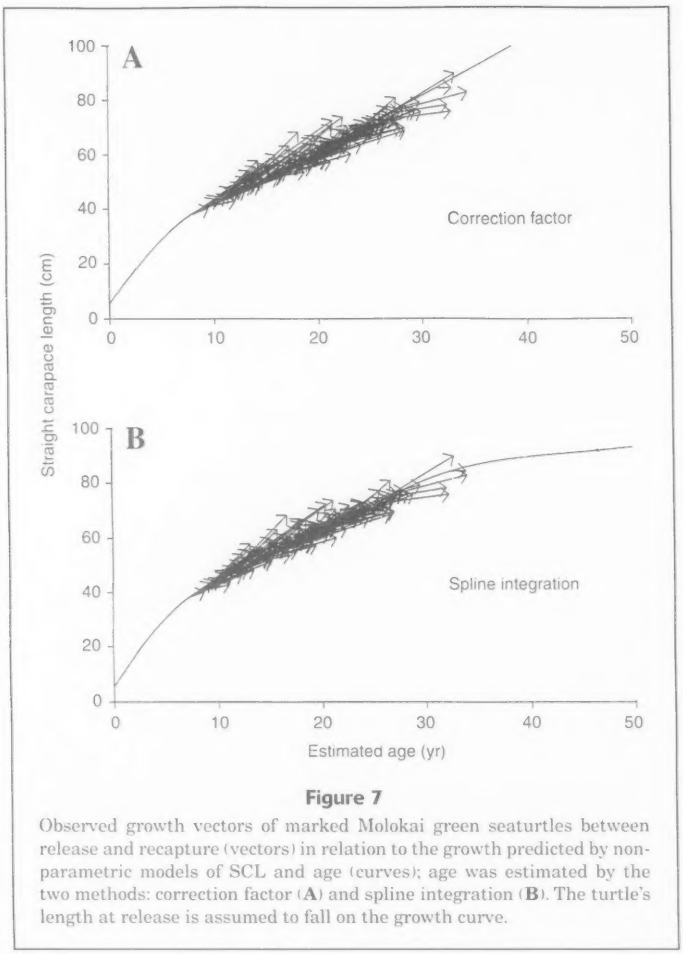

Figure 7

Observed growth vectors of marked Molokai green seaturtles between release and recapture (vectors) in relation to the growth predicted by nonparametric models of SCL and age (curves); age was estimated by the two methods: correction factor (**A**) and spline integration (**B**). The turtle's length at release is assumed to fall on the growth curve.

effects of fibropapillomatosis and gender on growth rates among the Hawaiian population.

Age-estimation methods

A key assumption of both the CF and SI methods is that each estimated humerus growth layer represents 1 year of growth. This assumption has been validated only recently (Hohn and Snover[1]). Hawaiian turtles tagged and injected with tetracycline have been recaptured, and these turtles show the appropriate number of LAGs for the years since their receipt of tetracycline. Furthermore, strong support is provided by the consistency of the growth model predictions with observed growth in tagged Molokai turtles. Additional justifications have been advanced in other studies of seaturtle humerus LAG formation (e.g. Zug and Glor, 1998; Coles et al., 2001).

[1] Hohn, A., and M. Snover. 2001. Personal commun. Beaufort Laboratory, Southeast Fisheries Science Center, Beaufort, NC.

Both the CF and SI methods require histological preparation and analysis of humerus sections. But they use the same skeletochronological data in independent and different ways to estimate the total number of humerus growth layers. The CF method assumes that a constant humerus growth rate (the "correction factor") applies to the resorption core regardless of the diameter of the core and despite the fact that periosteal increment width decreases with length of the turtle (Fig. 2). The correction factor, C, is estimated from a subset of the skeletochronological data taken from juvenile turtles only, i.e. excluding larger turtles likely to have narrower increments in the outer region of the humerus. Even so, the CF estimates of age for juvenile turtles appear to be biased upward (Fig. 5), suggesting that the constant correction factor also failed to reflect the effect of wider increments deposited in the early years of life. In age estimation, the CF method can be applied only to turtles displaying a complete set of periosteal layers, i.e. distinct LAGs, from the resorption core to the outer margin of the humerus.

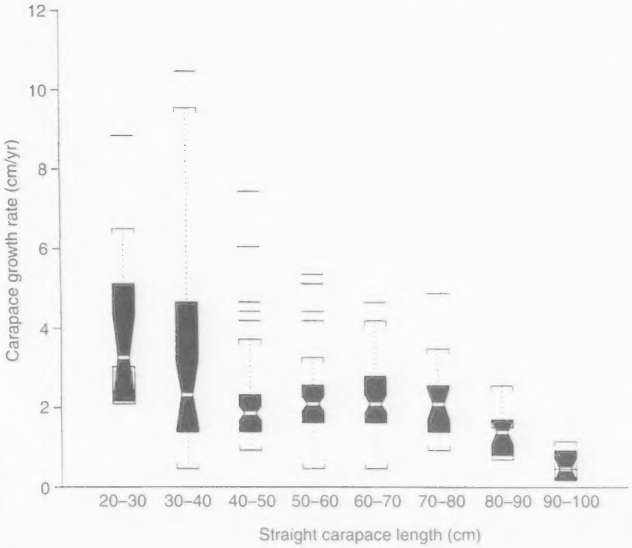

Figure 8

Variation of the growth rate estimates (SI-based) by carapace length class. Each box plot shows median (white bar), limits of 2nd and 3rd quartiles (solid notched box), range (brackets), and outliers (solid lines).

The SI method models increment-width variation over the entire distance from humerus center to outer margin by using a nonlinear, nonparametric smoother. The model is estimated from all available sample data with two or more LAGs and associated diameter measurements without regard to size of the turtle. The SI model can be applied to age all turtles for which the outside diameter of the humerus section has been measured.

In the skeletochronological sample we studied, the CF method gave age estimates significantly higher than the SI method for turtles of intermediate length (Table 1), but expected differences for such turtles were no greater than about 2 years. On the other hand, based on current data the CF-based model gives much lower age estimates than the SI-based model for turtles longer than about 86 cm SCL (Fig. 5). Thus although either method may suffice for aging juvenile Hawaiian green seaturtles, only the SI method appears to provide support for inferences about growth in turtles larger than about 80 cm. The CF method is computationally simpler, because it involves only linear regression rather than fitting and integrating a nonparametric smoother, and this consideration may recommend it to some users.

Based on our experience with Hawaiian green seaturtle data, the main issue in judging the two techniques appears to be the assumption with the CF method that humerus growth is linear. In reality, it is curvilinear, and the SI method explicitly models this curvilinearity. Moreover, the SI method makes fuller use of available humerus increment data than the CF method. Further comparisons of the methods with additional skeletochronological data sets are recommended.

Ecological précis

1 *Chelonia mydas* within the Hawaiian Islands is a component of the larger Indo-Pacific *C. mydas* gene pool, yet the nesting females of the Hawaiian population comprise a distinct genetic unit and contain a unique mtDNA haplotype (Bowen et al., 1992).

2 Except for the posthatching pelagic phase, the green seaturtles of the Hawaiian coastal waters are year-round residents, and all known individuals reproduce within the Hawaiian island chain, predominantly on the beaches of the Northwestern Islands at French Frigate Shoals (Balazs, 1998; Wetherall et al., 1999).

3 Skeletochronological age estimates indicate that Hawaiian juveniles exit the pelagic phase between the ages of 4 to 10 years.

4 In coastal waters, juveniles 10 years and older possess a relatively constant growth rate until about 28 to 30 years (approximately 80 cm SCL), then growth begins to slow as individuals attain sexual maturity.

5 The mean SCL of nesting females is 92 cm (range 81–106 cm; Balazs, 1980), suggesting ages of 30 or more years at first nesting for some individuals.

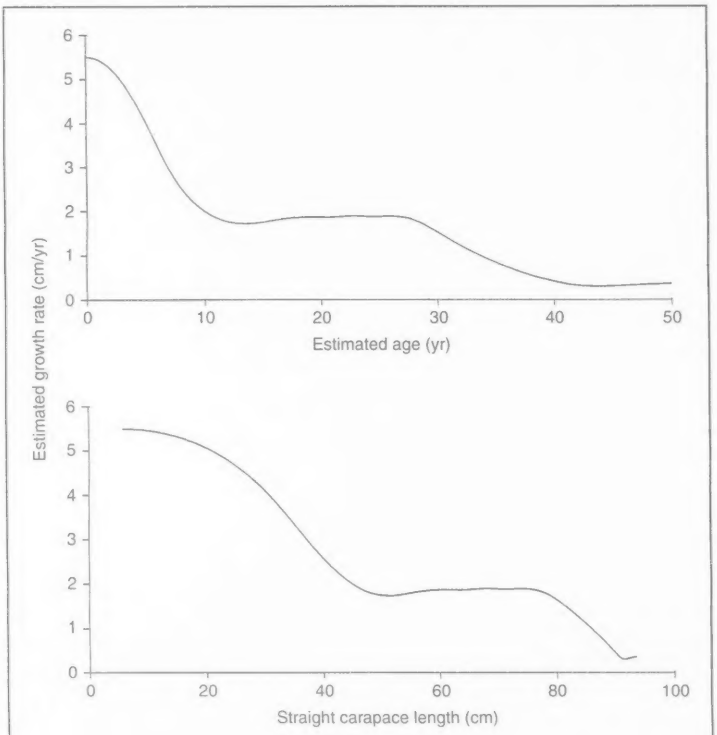

Figure 9

Growth rates of Hawaiian *Chelonia mydas* in relation to age and carapace length, estimated by taking first differences of the SI-based growth model.

Acknowledgment

We thank the following individuals and organizations for their valuable contributions to this research: A. Aguirre, D. Akaka, G. Antonelis, S. Eames, W. Gilmartin, S. Hau, D. Heacock, J. Kendig, R. Morris, W. Puleloa, L. Hallacher, W. Dudley, J. Coney, S. Patton, R. Sparks, M. Rice, G. Watson, M. Wisner, T. Work, the State of Hawaii Department of Land and Natural Resources, the Hawaii Preparatory Academy, Makai Animal Clinic, and the Marine Option Program of the University of Hawaii (Manoa and Hilo). George Zug thanks the NOAA-NMFS-SWFSC Honolulu Laboratory and SI/NMNH Department of Systematic Biology for encouraging and supporting his skeletochronological research.

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Estimates of lobster-handling mortality associated with the Northwestern Hawaiian Islands lobster-trap fishery

Gerard T. DiNardo
Edward E. DeMartini

Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2570 Dole Street
Honolulu, Hawaii 96822
E-mail address (for Gerard T. DiNardo): gdinardo@honlab.nmfs.hawaii.edu

Wayne R. Haight

Joint Institute of Marine and Atmospheric Research
School of Ocean and Earth Science and Technology
University of Hawaii, 1000 Pope Road
Honolulu, Hawaii 96822

The commercial lobster fishery in the Northwestern Hawaiian Islands (NWHI) is a distant-water trap fishery that targets the Hawaiian spiny lobster *(Panulirus marginatus)* and slipper lobster *(Scyllarides squammosus)*. The NWHI are an isolated group of islands, atolls, islets, reefs, and banks that extend 1500 nmi west-northwest of the main Hawaiian Islands from Nihoa Island to Kure Atoll (Fig. 1). Reported landings in the NWHI peaked at about 2,000,000 lobsters (spiny and slipper combined) in 1985, and then declined to about 38,000 lobsters from 1986 to 1995 (Fig. 2).

The NWHI lobster fishery is managed under the Fishery Management Plan for the Crustaceans of the Western Pacific Region (Crustaceans FMP) implemented in 1983 and developed by the Western Pacific Regional Fishery Management Council (WPRFMC). The National Marine Fisheries Service (NMFS) is responsible for stewardship of the resource and review and implementation of proposed management measures. A variety of management measures have been adopted in response to declining catches: a limited-entry fishing regime that limited the number of permit holders to 15; a prohibition on fishing from January through June when lobsters spawn; an annual catch quota system; a minimum legal tail width (TW) of 50 mm for spiny lobster and 56 mm TW for slipper lobster, which are close to the sizes at first maturity for these species in the NWHI; a prohibition on landing berried (ovigerous) females; and a requirement that traps be equipped with escape vents to reduce capture of undersize lobsters (WPRFMC[1]). Prior to 1996, fishermen were required to discard all berried and undersize lobsters, which were not counted against the catch quota.

The management plan assumed that escape vents allowed substantial numbers of undersize lobster to escape capture and that undersize and berried lobsters do not die during the discard process. Although research on lobster fisheries has found that escape vents effectively reduce the capture of undersize lobsters (Krouse, 1978; Fogarty and Borden, 1980; Harris, 1980; Everson et al., 1992; Skillman et al.[2]), considerable numbers of undersize (henceforth termed "sublegal") and berried lobsters are caught in the NWHI lobster fishery. Between 1983 and 1995 the reported lobster discard rate increased from 28% to 62% (Fig. 3), resulting from changes in the size- and age-structures of the populations and in the areas fished. The average size of spiny lobsters generally increased northwestward from Nihoa along the Hawaiian Archipelago (Uchida et al., 1980). Although as many as 16 banks within the NWHI have been fished, the spatial distribution of fishing effort has shifted to banks in the southeast of the Hawaiian Archipelago where there is a higher concentration of spiny lobsters.

Qualitative data collected during the early days of the fishery suggested that mortality associated with the handling and discarding practices of the NWHI commercial lobster-trap fishery might be high (Gooding, 1985; Gooding[3]). Unless discard mortality is explicitly considered, fishing policy decisions can be suboptimal, or worse. Where catch quotas are used, the total fishing-induced mortality of the population is greater than expected and can even result in recruitment overfishing. Using an equilibrium yield-per-recruit (YPR) model, Kobayashi[4] found that the reproductive potential of the NWHI lobster population more than doubled, and mean weight per individual increased by 22% in a retain-all fishery (all lobsters brought on deck were retained as catch) if the mortality rate of discarded lobsters was high (>75%). Based on these results, the observed high discard rate of sublegal and berried lobsters (62%), and the presumption that the

[1] Western Pacific Regional Management Council. 1995. Fishery management plan for the crustacean fisheries of the Western Pacific region, amendment 9. Western Pacific Regional Fishery Management Council, Honolulu, Hawaii, 227 p.

[2] Skillman, R. A., A. R. Everson, and G. L. Kramer. 1984. Prospectus escape vent experimental procedure for the spiny lobster fishery under management of the Magnuson Fishery Conservation and Management Act. Southwest Fish. Sci. Cent. Admin. Rep. H-84-13, unpubl. report, 11 p. Honolulu Lab., Southwest Fish. Sci. Cent., Natl. Mar. Fish Serv., NOAA, Honolulu, HI 96822-2396.

[3] Gooding, R. M. 1979. Observations on surface-released, sublegal spiny lobsters, and potential spiny lobster predators near Necker and Nihoa. Southwest Fish. Sci. Cent. Admin. Rep. H-79-16, unpubl. report, 8 p. Honolulu Lab., Southwest Fish. Sci. Cent., Natl. Mar. Fish Serv., NOAA, Honolulu, HI 96822-2396.

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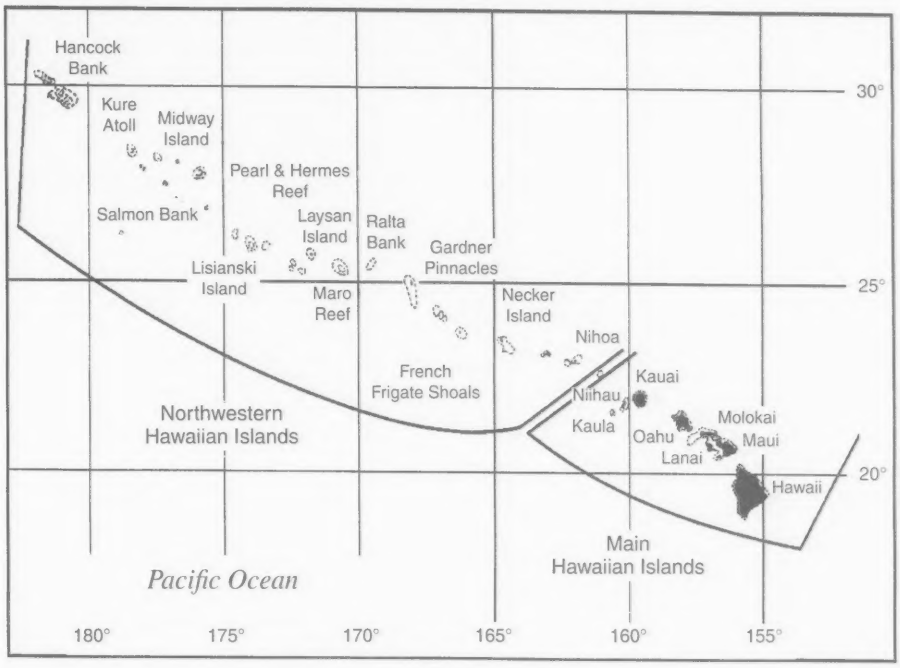

Figure 1
Map of the Hawaiian Archipelago.

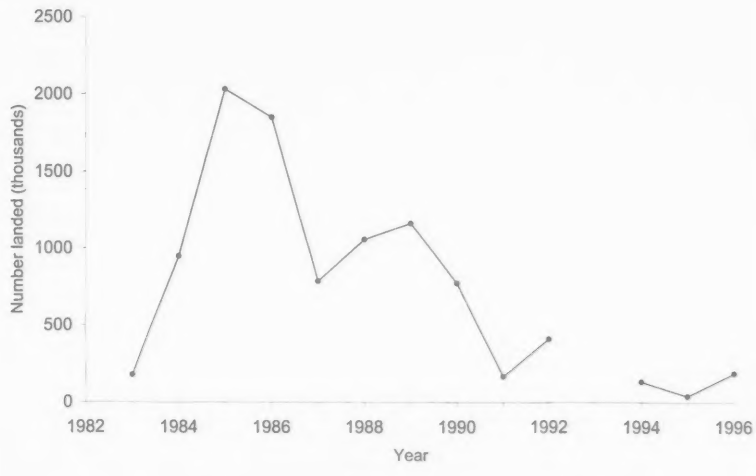

Figure 2
Annual commercial landings for the NWHI lobster fishery, 1983–96.

mortality rate of discarded lobsters is greater than 75%, the WPRFMC amended the Crustaceans FMP in 1996 to allow the retention of all lobsters caught in the NWHI commercial lobster-trap fishery subject to the quota on total catch (WPRFMC[1]). The WPRFMC also recommended that NMFS conduct experiments to assess mortality associated with possible handling and discarding practices.

This study reviews research conducted in the NWHI on fishery-induced mortality of sublegal and berried lobsters. The authors examined on-deck mortality of sublegal and

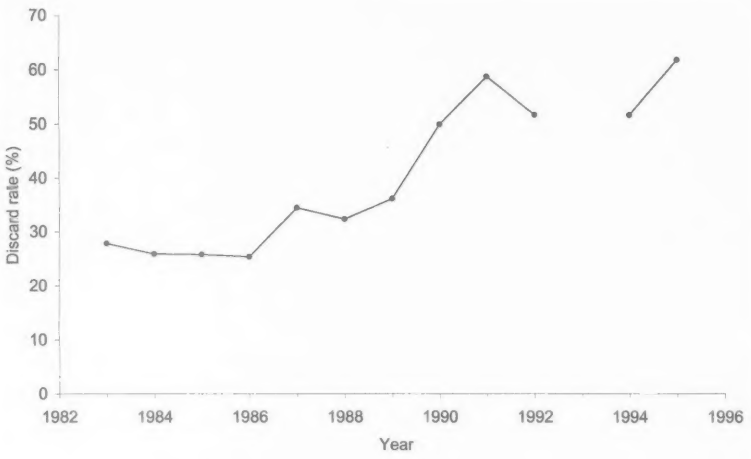

Figure 3

Annual estimates of the reported discard rate of lobsters in the NWHI lobster fishery, 1983–95.

berried spiny and slipper lobsters that occurred within two days after capture under handling methods known to have been used in the NWHI lobster-trap fishery.

Methods

Studies of handling-induced mortality (referred to as "handling mortality" in the remainder of this note) for spiny lobster were conducted at Necker Island onboard the NOAA ship *Townsend Cromwell* during the NMFS Honolulu Laboratory's 1996 NWHI lobster survey from 21 to 26 June 1996 and for slipper lobster at Maro Reef from 4 to 11 July 1996 (see Fig. 1). These locations were chosen because of their historically high lobster catches and their overall importance to the commercial lobster fishery over the past 13 years.

Handling mortalities were estimated for two handling methods: "dry" and "wet." The effects of on-deck exposure time on handling mortality were also estimated for spiny lobsters handled by the dry method. We defined a particular combination of factors (method and exposure time) as an experimental treatment. For dry treatments, lobsters were held on deck in 30-gallon containers without water and in direct sunlight for 1, 2, or 3 hours. In the wet treatment, lobsters were held on deck for 3 hours in shaded 30-gallon containers with circulating seawater. The 2- and 3-h dry treatments represent prevailing commercial fishing practices (Anderson[5]), whereas the 1-h dry treatment and the 3-h wet treatments represent possible handling alternatives or mitigative measures.

Spiny and slipper lobsters were collected in baited commercial lobster traps and sorted (legal, sublegal, and berried). All sublegal and berried lobsters were held in tanks of circulating water until a sufficiently large paired experimental treatment sample (n=200 lobsters) was collected. Experiments with the 3-h wet and dry treatments were done first, followed by experiments involving 1- and 2-h dry treatments. For each treatment, 100 lobsters (sublegal and berried) were randomly chosen from the tank and placed into two 30-gallon treatment containers (dry or wet), 50 lobsters/container. After the exposure time (1, 2, or 3 hours), lobsters were removed from the treatment containers, their condition recorded as active (i.e. lobsters were capable of tail flexion), weak (incapable of tail flexion but able to move appendages when prodded), or dead. Five lobsters were placed in each of 20 lobster-holding traps (commercial lobster traps with sealed entrances) and held in two 1320-gallon baitwells with recirculating seawater (21 gallons/minute) for 2 days. It was assumed that the 2-d holding period would allow ample time for latent effects from a treatment to manifest and that each lobster holding trap was a replicate (n=20 replicates/treatment). To check for possible baitwell effects, five control traps, each containing five previously untreated lobsters, were placed in the baitwells (two traps in the port baitwell and three traps in the starboard baitwell) at the beginning of the holding phase, and their condition was recorded at the beginning and end of the holding phase. At the conclusion of the holding period, the condition of the treated lobsters was again assessed.

Handling mortality for each treatment was computed as the arithmetic mean of the percent mortality (dead/total or (dead + weak)/total—see below) observed in the 20

[5] Anderson, P. 1997. Personal commun. University of Hawaii, Marine Option Program, 1000 Pope Road, Honolulu, HI 96822. Kazama, T. 1997. Personal commun. Honolulu Laboratory, Southwest Fisheries Science Center, 2570 Dole Street, Honolulu, HI 96822-2396.

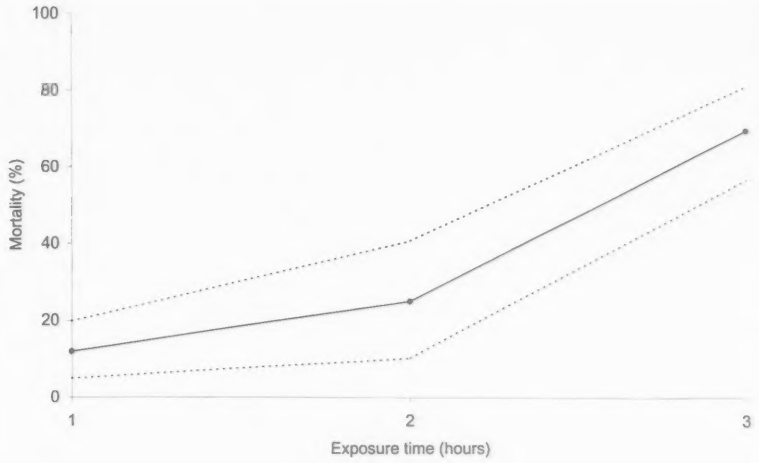

Figure 4

Handling mortality (dead/total) estimates for spiny lobster subjected to 1-, 2- , and 3-h dry treatments. Dashed lines indicate the 95% confidence limits.

treatment replicates. Randomization resampling was used to evaluate estimates of handling mortality. Approximate lower and upper 95% confidence limits for handling mortality were computed as the 2.5% and 97.5% percentiles of the bootstrap distributions by using the computer program RT (Manly, 1994).

Results

Spiny lobster

Spiny lobster sample sizes by discard category were sublegal (n=84–88) and berried (n=12–16) (Table 1). All spiny lobsters subjected to the 3-h wet treatment were active at the conclusion of the 2-d baitwell holding period. For dry treatments, the number of active spiny lobsters decreased with increasing exposure time, whereas the number of dead lobsters increased with increasing exposure time. All control lobsters were active, indicating no baitwell holding effects.

Handling mortality (dead/total) for the dry treatment ranged from 12% for the 1-h treatment to 70% for the 3-h treatment (Fig. 4) and did not differ between berried and unberried lobsters (P>0.05). Pooled dead and weak lobsters resulted in a handling mortality that ranged from 16% for the 1-h treatment to 77% for the 3-h treatment (Fig. 5).

Slipper lobster

Handling mortalities for slipper lobster were estimated only for the 3-h dry and wet treatments. Mechanical failure of the baitwell recirculating water pumps during the first 3-h paired dry and wet experiments forced us to reduce the baitwell holding time to 1 day. After the baitwell pumps failed, we repeated the 3-h dry treatment with a 1-d holding period, suspending the holding and control traps 3 m below the sea surface from the *Townsend Cromwell*.

Table 1

Spiny and slipper lobster sample sizes by discard category for each treatment. NB = nonberried and sublegal; B = berried.

	Spiny lobster		Slipper lobster	
Treatment	NB	B	NB	B
1 hour dry	84	16	—	—
2 hours dry	88	12	—	—
3 hours dry	87	13	87–89	11–13
3 hours wet	88	12	81	19

Slipper lobster sample sizes by discard category (sublegal and berried) for each treatment are shown in Table 1. Most slipper lobsters subjected to the 3-h wet treatment were active at the end of the 1-d holding period. For the 3-h dry treatment, the number of dead lobsters ranged from 14 to 39, and the number of active lobsters ranged from 56 to 83. All control lobsters were active, indicating no baitwell holding effects.

Slipper lobster handling mortalities for the 3-h dry treatment ranged from 14% to 39% with an average estimate of 27% and were unrelated to berried condition (P>0.05). Estimates of handling mortalities with weak and dead lobsters combined ranged from 17% to 44%, with an average of 31%. Handling mortality for the 3-h wet treatment was 1%.

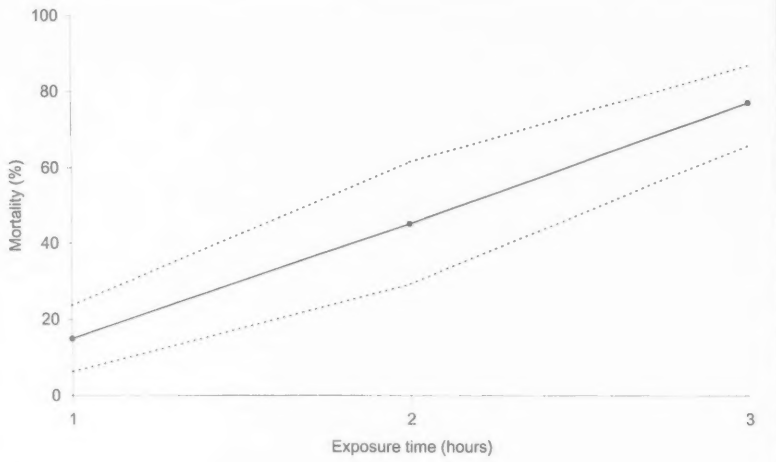

Figure 5

Pooled handling mortality ((dead + weak)/total) estimates for spiny lobster subjected to 1-, 2-, and 3-h dry treatments. Dashed lines indicate the 95% confidence limits.

Discussion

Many factors affect the survival of lobsters discarded in commercial trap fisheries, including capture, handling, and discarding processes. In our experiment we focused on handling factors to assess their impacts on mortality in the NWHI commercial lobster fishery.

If the 2- and 3-h dry experimental treatments typify commercial handling practices, then the mortality of discarded spiny lobster from handling practices on commercial vessels is extreme, ranging from an average of 25% to 45% and 70% to 77%, respectively, depending on how data are pooled. Handling mortality for slipper lobster also appears high (estimated at 31%) but is considerably less than that for spiny lobster; thus spiny lobsters may have a lower handling tolerance than slipper lobsters.

Although there are no published estimates of handling mortality for *P. marginatus* and *S. squammosus*, studies on other lobster species suggest that handling mortality in the NWHI lobster fishery is high. Lyons and Kennedy (1981), reporting on *P. argus*, estimated that 12.3% of lobsters died after 30 minutes of exposure to direct sunlight and an average 24.1% after 1–4 hours of exposures. They also found that lobsters exposed for 2–4 hours tended to die within a week following exposure, whereas those exposed for only 1 hour survived longer. Laboratory experiments by Brown and Caputi (1983) on small western rock lobster, *Panulirus cygnus*, exposed to direct sunlight resulted in an expected time to 50% mortality that decreased with increasing temperature, ranging from 233 minutes at 27°C to 99 minutes at 31–35°C. Time to 50% mortality was 387 minutes for lobsters held in the shade at 26.5–32°C.

Handling mortality, however, represents only a portion of the total mortality of discarded lobsters resulting from their capture, shipboard processing, and subsequent release in the NWHI. Additional mortality resulting from habitat displacement, predation, and other factors associated with discarding might result in total discard mortality estimates that approach 100%. Qualitative evidence suggests that discarded lobsters are subject to high predation from the giant trevally, *Caranx ignobilis*, which aggregate around vessels during fishing operations (Gooding, 1985).

Sorting and discarding lobsters immediately after they are placed on deck appears to reduce total discard mortality. The discarded lobsters would need to be returned to the general vicinity of their capture and as close to the sea floor as possible to avoid the gauntlet of predators in the water column. Brown and Caputi (1986) reported a reduction in recapture rates of displaced undersized rock lobsters compared with nondisplaced rock lobsters and related the reduction directly to predation mortality.

Adoption of the retain-all fishery by the WPRFMC in 1996 significantly reduced fishery-induced handling mortality. Although sporadic discarding occurs, current discard rates are less than 1% and will have no detectable consequence at the population level. The research does, however, provide insight into past fishery-induced handling impacts, which likely contributed to the decline in NWHI lobster catches. If future management again reverted to mandatory discarding practices, this research provides information to assess its impact on fishery-induced mortality. However, to fully understand the synergistic effects of catching, handling, and discarding practices on mortality in the NWHI lobster fishery, additional research to assess the impacts associated with shipboard sorting and releasing (e.g. postrelease predation) is required.

Acknowledgments

Robert Moffitt, Donald Kobayashi, Jerry Wetherall, and the anonymous referees provided helpful comments on the draft, for which we are very grateful. We also acknowledge the crew of the *Townsend Cromwell* and the scientific staff who worked to ensure that good biological information is available for analyses such as this.

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An evaluation of pop-up satellite tags for estimating postrelease survival of blue marlin (*Makaira nigricans*) from a recreational fishery*

John E. Graves
Virginia Institute of Marine Science
College of William and Mary
Rt. 1208 Greate Road
Gloucester Point, Virgina 23062
E-mail address: graves@vims.edu

Brian E. Luckhurst
Division of Fisheries
Department of Agriculture and Fisheries
P.O. Box CR 52
Crawl CRBX, Bermuda

Eric D. Prince
National Marine Fisheries Service
75 Virginia Beach Drive
Miami, FL 33146

Blue marlin (*Makaira nigricans*) represent an important commercial and recreational resource throughout tropical and subtropical oceanic waters. In the Atlantic Ocean, blue marlin are managed as a single, oceanwide stock. In the most recent assessment of Atlantic blue marlin (ICCAT, 2001), the Standing Committee for Research and Statistics (SCRS) of the International Commission for the Conservation of Atlantic Tunas (ICCAT) estimated the current biomass of blue marlin to be about 40% of that required for maximum sustainable yield (MSY). Furthermore, the assessment indicated that the current level of fishing mortality (F) was about four times higher than F_{MSY} and that catch levels in recent years were more than twice the equilibrium yield, contributing to a further decline of the overexploited stock. Based on the most recent stock assessment, fishing-induced mortality must be reduced by about 60% to halt the decline of the stock (Goodyear, 2000).

The greatest source of billfish (Istiophoridae) mortality occurs as a result of incidental catches by longline gear deployed for tunas and swordfish (ICCAT, 1997, 2001). These highly migratory species co-occur in the subtropical and tropical epipelagic environment, and all are vulnerable to the pelagic longline. Not all billfish are dead at the time of capture (haulback) on longline gear; data from observers on vessels in the Venezuelan industrial longline fishery indicate that about 49% of blue marlin caught on pelagic longline gear are alive at the time of capture (Jackson and Farber, 1998).

To reduce billfish mortality ICCAT in 1997 required nations to reduce their landings of Atlantic blue marlin by 25% from 1996 levels. Furthermore, the ICCAT SCRS has recommended that the Commission consider requiring the release of all live billfish taken on longline gear (ICCAT, 1997, 2001). It is believed that such a management measure would be more acceptable to member nations than an overall reduction in longline effort that would also reduce catches of target species. However, representatives from several nations have pointed out that there are not sufficient data to estimate postrelease survival of billfish; therefore the conservation impact of a recommendation requiring live released fish cannot be evaluated. In fact, low recovery rates of billfish tagged and released with conventional tags by recreational and commercial fishermen (<2%; Jones and Prince, 1998; Ortiz et al, 1998) are consistent with high postrelease mortality. However, factors such as tag shedding and failure to report tag recaptures could also account for low rates of tag returns (Bayley and Prince, 1994; Jones and Prince, 1998). Clearly, data are needed to support or refute the hypothesis that the release of live billfish would significantly eliminate fishing mortality of blue marlin (Graves et al.[1]).

Acoustic tracking studies designed to investigate billfish physiology and behavior have provided insights into the postrelease survival of billfish taken on recreational gear. Specifically, observed and inferred mortalities during the course of the acoustic tracks indicate that not all released billfish survive (reviewed in Pepperell and Davis, 1999). Unfortunately, it is not possible to estimate levels of postrelease mortality of billfish from previous acoustic tracking studies for several reasons. First, owing to the high cost of ship and personnel time, relatively few animals have been investigated in acoustic tracking studies. Second, because ocean conditions can deteriorate quickly, many of the acoustic tracks were for less than 12 hours duration, providing a limited opportunity to observe mortality after 12 hours. Third, billfish were caught and subsequently tracked under a variety of conditions, making cross-study comparisons difficult. Finally, an estimate of postrelease mortality rates resulting from acoustic studies may be biased because in some cases only healthy fish were selected to carry acoustic transmitters.

The development of pop-up satellite tag technology may present a possible means to estimate postrelease mortality of billfish. Although relatively expensive pop-up satellite tags reduce the need to use a tracking vessel to follow

* Contribution 2416 of the Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA 23062.

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billfish on the high seas. Pop-up satellite tags are capable of recording environmental variables over predefined intervals, of detaching from an animal at a designated time, floating to the surface, and of transmitting the stored data to a satellite. Until now, these tags have been deployed primarily on bluefin tuna for relatively long durations (up to nine months) to determine movement patterns (Block et al., 1998a; Lutcavage et al., 1999). Recovery of tag data has been very good in most cases, with some reported rates in excess of 90% (Block et al., 1998a; Lutcavage et al., 1999). These results suggest that the technology may be well suited for shorter term studies, including the determination of postrelease survival. In this paper we present the results of a preliminary study to evaluate the feasibility of applying pop-up satellite tag technology to estimate short-term survival of blue marlin. We also include a brief analysis of the movement and behavior of blue marlin that we inferred from the pop-up tagging results.

Materials and methods

Pop-up satellite tags

The Microwave Telemetry, Inc. PTT-100 pop-up satellite tag was used in this study. The tag can withstand a pressure of 1000 psi (equivalent to a depth of about 650 meters) and is sufficiently small (38 cm by 4 cm diameter) that it would not appear to impose a major drag on a large marine teleost, such as blue marlin (Block et al., 1998a). Tags were programed to measure water temperature every hour and record the mean value for each two-hour period for a total of 61 cycles (122 hours). Inclinometer values were taken every two minutes and summed for the periods before tag detachment (pre-pop-up) and after tag detachment (post-pop-up). For each period the inclinometer started with an initial value of 128. If at the time of measurement (every two minutes) the tag was oriented below 30 degrees above horizontal, a value of one was subtracted from the total. If the tag was above 30 degrees above horizontal at the time of measurement, the inclinometer total was increased by one, but could not exceed 255. Final values below 255 indicated sufficient forward propulsion such that the positively buoyant tag was depressed below 30 degrees above horizontal for certain periods, demonstrating forward propulsion.

All nine tags were programed to detach from the fish 122 hours after activation, at which time the memory within each tag would contain 61 direct temperature measurements and the pre-pop-up inclinometer value. The five-day attachment period of the pop-up tag was chosen, in part, as a result of a review of data from conventional tag-recaptured blue marlin in the Cooperative Tagging Center (CTC) database (E. Prince, unpubl. data). Of the 160 blue marlin tag returns in CTC that have been validated, ten individuals were recaptured within five days of release, suggesting that some blue marlin are able to survive the catching and tagging event and commence feeding again within a few days. In addition, acoustical tagging studies have shown high survival rates of different marlin species in the first 1–2 days following release, demonstrating that mortality, when it occurred, generally happened within the first 48 hours of release (Pepperell and Davis, 1999). With these considerations in mind, we assumed that the five-day period of tag attachment was an adequate period for catch and release mortality to be expressed. As indicated by Goodyear (in press), the duration of this type of experiment should be the minimum number of days necessary to account for postrelease mortality events. Longer periods would allow for greater influence of tag shedding, tag malfunction, and natural mortality, all of which could compromise estimates of postrelease survival.

Tag deployment

Pop-up satellite tags were activated and tested at the start of each fishing day. Blue marlin were caught southwest of Bermuda in the vicinity of Challenger and Argus Banks on standard recreational gear for the blue marlin fishery in Bermuda (130 lb test line) by using trolled high-speed lures or skirted dead baits (in most cases with two hooks). All hooks employed in this study were "J" hooks (no. 16/0–20/0). We tagged the first nine fish available to us. Six blue marlin were caught on the vessels we were aboard. Three individuals were taken on other vessels and transferred to the tagging vessel after the fish were brought to leader (brought to the boat): one blue marlin was caught and attached to a drifting buoy until the tagging vessel, which was several miles away, could gain access to the fish; and two fish were directly transferred after capture from the fishing vessel to the tagging vessel by using a procedure described in Block et al. (1998b).

Once fish were brought to leader (reeled to the side of the boat), quieted and secured, the pop-up satellite tag and a conventional (streamer) tag were deployed. Pop-up satellite tags were attached to one end of a 400-lb (182 kg) test monofilament leader about 18.5 cm in length, with an outside diameter of 1.8 mm. The other end of the leader was attached to a double barb nylon anchor (about 33 mm long and 10 mm wide) made of medical-grade nylon. The anchors were implanted by using a stainless steel tag applicator modified to accomplish placement to a depth of about 10 cm into the dorsal musculature, about 10 cm posterior and 5 cm below the base of the peak of the first dorsal fin (Fig. 1). Hook location, as well as observations on foul-hooking (tissue damage, bleeding, etc.), were noted at the time of hook removal.

Analyses

After detachment from the animal, the positively buoyant tags floated to the surface and began transmitting data to satellites of the Argos™ system. Position information and sections of the temperature and inclinometer data were captured with each satellite pass and transmitted to a ground station and ultimately to the investigators by the internet. Data were analyzed to determine net movement from the point of detachment to the point when the tag popped-up (usually the first tag transmittal; however, if the first satellite pass was near the horizon, the location of the second transmittal was used to obtain greater accu-

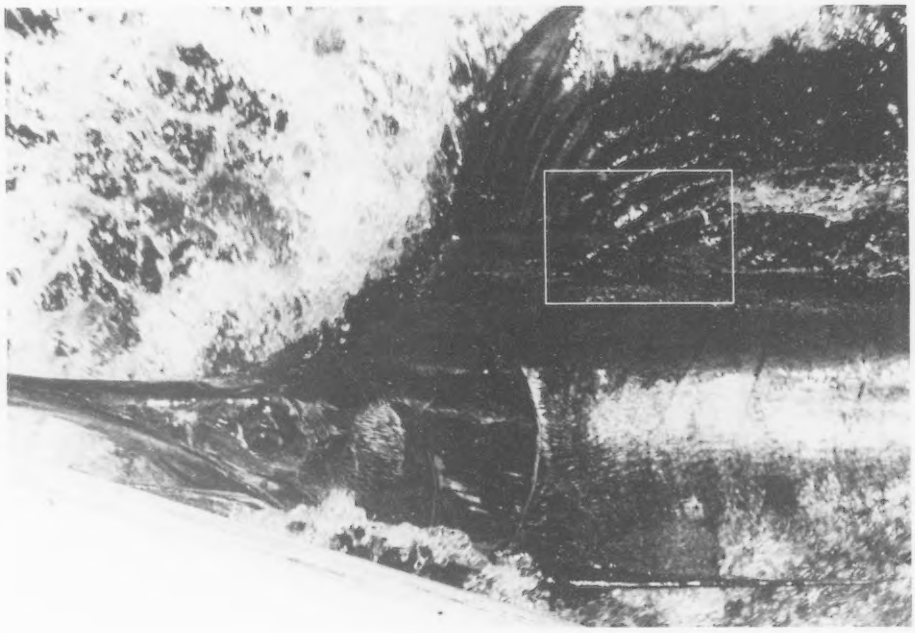

Figure 1

Blue marlin with pop-up satellite tag attached. The tag is located below the anterior portion of the dorsal fin (within outlined area).

racy). Water temperature was determined from temperature sensor readings by using a calibration provided by the manufacturer. Depth was estimated from water temperature values by using temperature and depth relationships provided by the Bermuda Biological Station for Research, which maintains an oceanographic sampling station (station S) about 13 miles (24 km) to the southeast of the island.

Results and discussion

Nine blue marlin, with estimated weights ranging from 150 to 425 lb (68 to 193 kg), were tagged between 25 July and 11 August 1999 (Table 1). Four specimens were below the minimum size for tagging recommended by the tag manufacturer (200 lb or 90.9 kg). Fight times ranged between 15 and 35 minutes. Seven fish were initially hooked in the jaw, and two were "foul-hooked" (i.e. outside the jaw and mouth): one in the operculum and one in the dorsal musculature. After tag placement, but before release, one fish that was originally hooked in the jaw became foul-hooked in the ventral musculature. Three of the nine fish were transferred to the tagging vessel after capture. Fish generally quieted down shortly after being brought to the side of the vessel, which maintained a headway of 4–5 km/h during the tagging operation. Only a few minutes were required to implant the satellite and conventional tags, photograph the fish, estimate weight, measure lower jaw fork length (most individuals), and remove the hook. Condition of the fish varied, and three individuals required resuscitation prior to release.

Eight of the nine tags became detached from their respective host fish after five days, floated to the surface, and transmitted to the Argos™ satellite system. Based on the first accurate location of the tags, net displacements ranged from 40 to 134 nmi (72–248 km) with a mean linear displacement of 90 nmi (167 km) for each individual (Fig. 2). These values are in the range reported for blue marlin by Block et al. (1992) who followed six blue marlin with acoustic transmitters for periods of one to five days. They noted individual total movements (as opposed to net displacements) of 253 km in about three days, 100 km in five days, and four animals with movements of less than 100 km over the course of the respective tracking periods.

Individual marlin in our study dispersed in all directions from their point of release (Fig. 2). The blue marlin tracked by Block et al. (1992) and Holland et al. (1990) in Hawaiian waters moved away from the point of capture in several different directions. However, the authors noted an orientation of movements to the coastline of the Hawaiian Islands. Our releases were farther offshore and an affinity to the Bermuda coastline was not evident from the net movement data.

Depending on the time of tag activation and the time of tag deployment, up to 61 direct water temperature readings, taken every two hours, were obtained for each blue

Table 1

Pop-up satellite tag deployment information. "Transfer" indicates whether a fish was moved between vessels after capture to allow tagging. "Resuscitation" indicates the time spent to move a blue marlin through the water after capture until it could swim off under its own power. Tag no. 24040 failed to report.

Tag no.	Deployment date	Deployment hour	Fight time min.	Transfer (yes/no)	Hook location	Estimated weight (lb)	Resuscitation (no/yes—time)
24519	25 Jul 1999	1610	25	yes	jaw	400	no
24059	28 Jul 1999	1110	35	yes	jaw and ventral musculature	200	no
24522	1 Aug 1999	1030	20	yes	jaw	175	no
24520	2 Aug 1999	1015	15	no	jaw	180	no
24033	2 Aug 1999	1245	30	no	jaw	425	yes–10 min.
24040	2 Aug 1999	1500	17	no	jaw	200	no
24523	3 Aug 1999	1550	15	no	operculum	150	yes–8 min.
24527	11 Aug 1999	1255	15	no	jaw	350	no
24029	11 Aug 1999	1340	23	no	dorsal musculature	150	yes–3 min.

marlin (Fig. 3). Temperature readings demonstrated that tagged individuals spent the majority of their time at temperatures above 26°C (Fig. 4). The maximum temperature range recorded for any of the eight individuals was 9°C (22–31°C, tag no. 24033). Block et al. (1992), using acoustic tracking, determined that the six blue marlin which they tracked spent half of their time in the upper 10 m of the water column in water temperatures 25–27°C, and Holland et al. (1990) reported that blue marlin in waters off Hawaii remained at temperatures of 26° or greater.

Differences in thermal histories were evident among the individuals in our study. Blue marlin no. 24029 (Fig. 3G) spent the vast majority of time at temperatures equal to that of the surface waters (30–31°C). In contrast, individual no. 24527 (Fig. 3H) spent much less time in the warmer surface waters and repeatedly moved up and down in waters between 23° and 31°C. Several individuals appeared to remain at or very near the surface for extended periods, evident in Figure 3 as a continuous string of temperature readings at or slightly above 30°C. An analysis of the data examining diurnal-nocturnal periods with temperature (inferred depth) indicated a high level of variability between individuals and no clear pattern was apparent (Fig. 3). In contrast, Holland et al. (1990) determined that blue marlin spent a higher proportion of their time (~50%) in the upper 10 m at night than during the day (~25%).

It was possible to infer swimming depths of blue marlin by comparing water temperature values with the temperature-depth profiles at station "S" provided by the Bermuda Biological Station for Research.[2] All blue marlin entered cooler waters at various times during the five-day period, with excursions to depths as great as 40 meters. Temperature records were consistent with the tagged blue marlin actively undertaking vertical movements in the upper 40 meters of the water column. However, six of the eight fish spent >75% of their time in the upper 10 m of the water column for the five-day duration of the study. If the data from all eight fish are pooled, this yields a mean value of 79.9% (SD 15.8%) of the time spent in this zone. This is a higher percentage of time spent in the upper 10 m than that observed by Block et al. (1992), who reported that fish spent about half of the time in this zone. However, this comparison should be viewed with some caution because the Block et al. (1992) data were based on continuous tracking, whereas each data point in our analysis was the average of two hourly measurements.

All post-pop-up inclinometer values were 254 or 255, where 255 represented the maximum (vertical) inclinometer value expected for an upright, floating tag. Pre-pop-up inclinometer values ranged from 203 to 251, with three individuals at 233 and four between 247 and 251. These values indicate tags were inclined at an angle below 30 degrees above horizontal for more than 40% of the 1830 sampling times for each individual, and are consistent with sufficient forward propulsion to depress the positively buoyant tag more than 60 degrees from vertical. There was no correlation between pre-pop-up inclinometer values and net displacement. The fish with the largest net displacement (no. 24059) had the second highest inclinometer value. This was not unexpected because the difference between the lowest and highest pre-pop-up inclinometer values represents a minor difference in the time the tag was depressed below 30 degrees above horizontal. Also, the relationship between total movement and net displacement could be quite different for different individuals.

Three different lines of evidence provided by the pop-up satellite tags (net movement, water temperature, and tag inclination) each suggested that at least eight of the

[2] Although this station is situated 24 km to the southeast of the island, similar temperature-depth profiles would be expected for the general region (Johnson, R. 2000. Personal commun. Bermuda Biological Station for Research, 17 Biological Lane, Ferry Reach, St. George's GE01 Bermuda). This allowed us to use the station S profiles to infer swimming depth, realizing that, depending on when an animal was tagged and where it moved, there would be some differences for which we could not account.

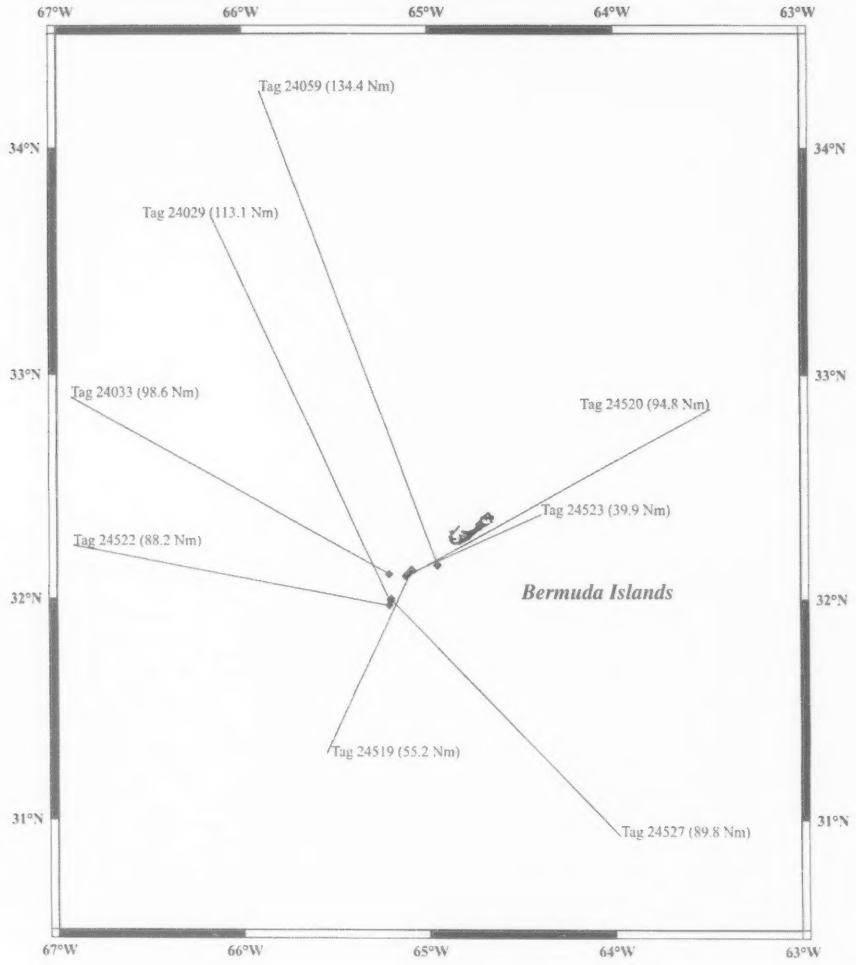

Figure 2

Map showing points of release (squares) and points of recovery (end of straight lines) for eight of nine blue marlin equipped with pop-up satellite tags near Bermuda, 25 July–11 August 1999. The pop-up satellite tag number for each fish and straight line distance between point of release and geolocation where tag transmitted data to the Argos satellite (given in parentheses) are provided.

nine blue marlin caught on recreational gear survived for five days following capture, tagging, and release events. The net movement data indicated a broad dispersal of the eight fish in different directions that cannot be explained by local currents. In contrast to the differing direction of movement, the net displacements of the eight fish were fairly similar. The mean displacement of 89.25 nmi over a five-day period, compares favorably with blue marlin swimming velocities of 1–2 nmi/h reported from acoustic tracking studies (Holland et al., 1990) and is consistent with the constant slow swimming of the individuals. Although currents could have accounted for some of the net displacement, inclinometer values indicated that all eight individuals were actively swimming.

The water temperature measurements indicated that each blue marlin actively undertook dives into cooler water throughout the course of the five days. All eight individuals spent the vast majority of their time in waters with temperatures of 26°C or greater, and no readings below 22°C were recorded.

The successful data recording, tag detachment, and transmission of eight of the nine pop-up satellite tags begs the question of what happened to the one tag that failed to report. It is not possible to distinguish between the postrelease mortality of a tagged blue marlin and the mechanical failure of a pop-up satellite tag. If a marlin dies and sinks in deep water, the attached pop-up satellite tag eventually will be crushed by increasing hydrostatic pressure.

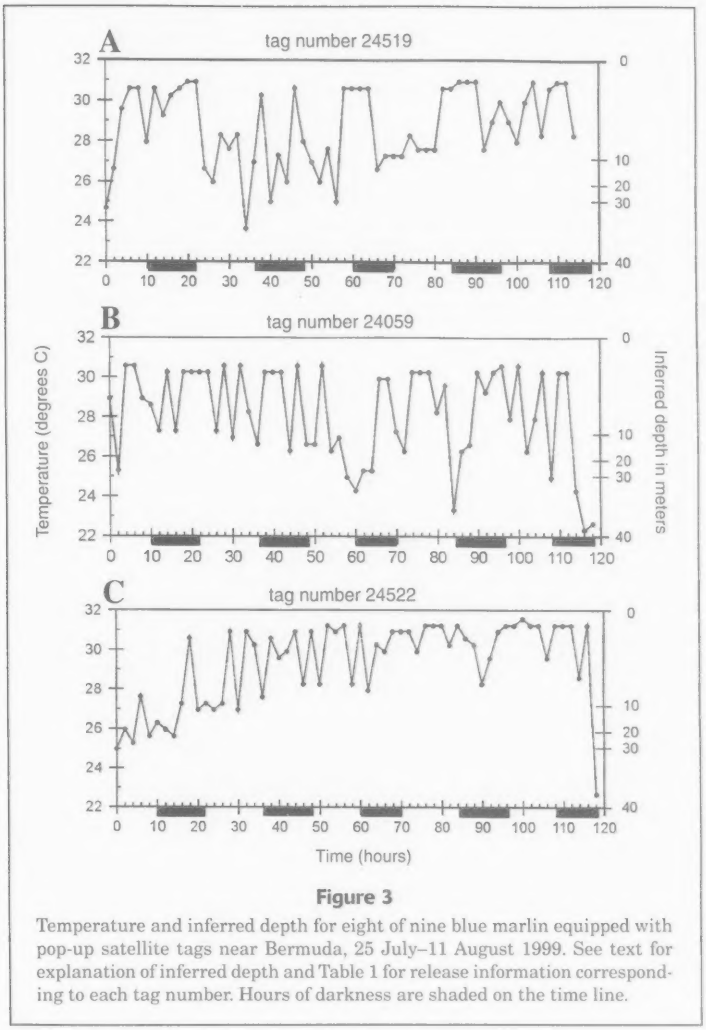

Figure 3

Temperature and inferred depth for eight of nine blue marlin equipped with pop-up satellite tags near Bermuda, 25 July–11 August 1999. See text for explanation of inferred depth and Table 1 for release information corresponding to each tag number. Hours of darkness are shaded on the time line.

The blue marlin whose tag did not report (tag no. 24040, Table 1) was hooked in the jaw, caught in less than 20 minutes, did not require resuscitation, was quickly tagged, and actively swam away from the boat when released. Shark predation on released billfish has been reported (Holland et al., 1990; Pepperell and Davis, 1999); therefore mortality cannot be excluded despite the apparent vigorous condition of the fish. Failures in component subsystems could account for the failure of reporting from a pop-up tag. A detailed analysis of the reliability of each tag component could be undertaken, but several factors external to the tag could also result in a failure of reporting. Tag manufacturer innovations and upgrades of the systems will allow researchers to better identify mortalities, but they will not completely solve the problem of discriminating between tag failure and fish mortality. Nonreporting tags would have significant consequences for efforts to make ocean-wide estimates of postrelease survival. The ability to account for all pop-up satellite tags deployed is directly related to the accuracy of the resulting estimates of postrelease survival (Goodyear, in press). Nonreporting satellite tags introduce uncertainty that cannot be quantified in the estimates of postrelease survival, thus compromising meaningful conclusions. Excluding nonreporting tags from the analysis decreases precision of the estimate, and including mortalities biases the survival estimate downward. Further, any extension of the 5-day pop-up period to allow study of possible delayed effects of tagging should involve careful consideration of the benefits and the liabilities that longer durations might have on estimating postrelease survival (Goodyear, in press)

Successful tagging and reporting of pop-up tags from four fish under 200 lb (90.9 kg) indicate that the size and design of the PTT-100 tag is tolerated by smaller blue mar-

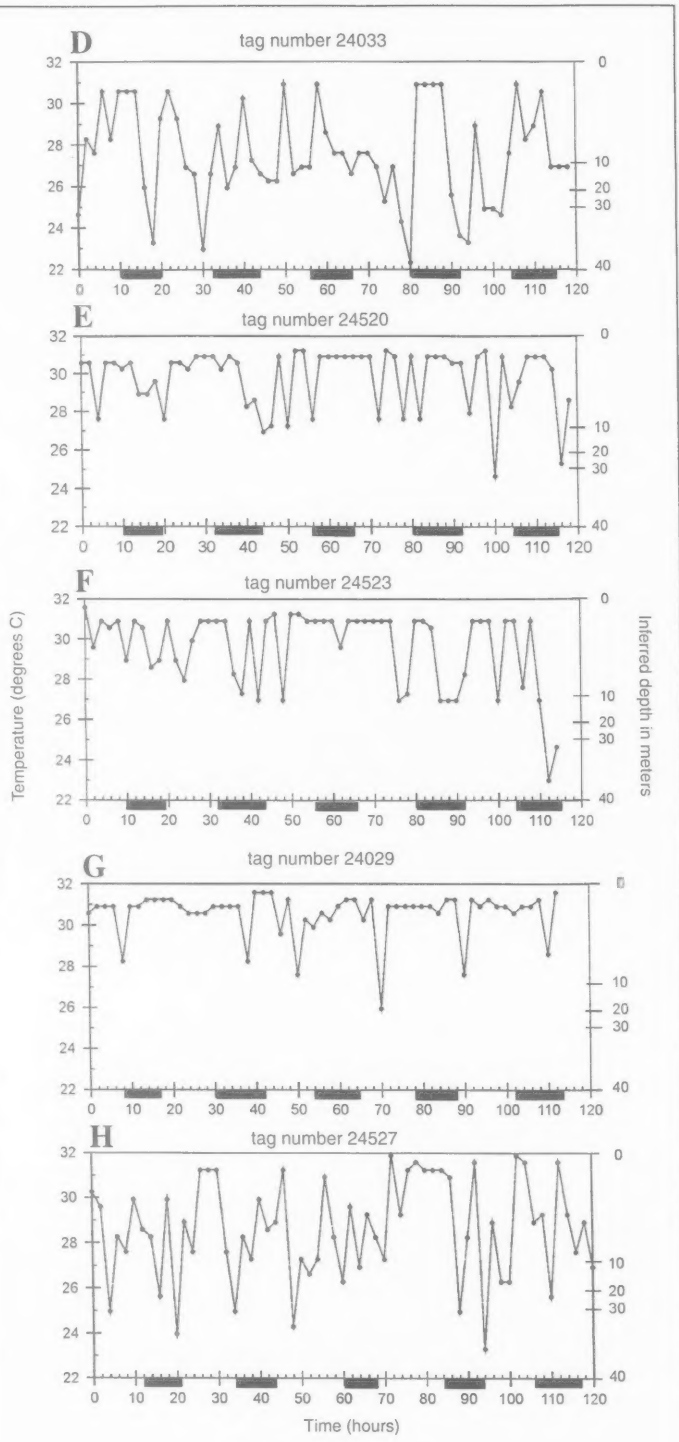

Figure 3 (continued)

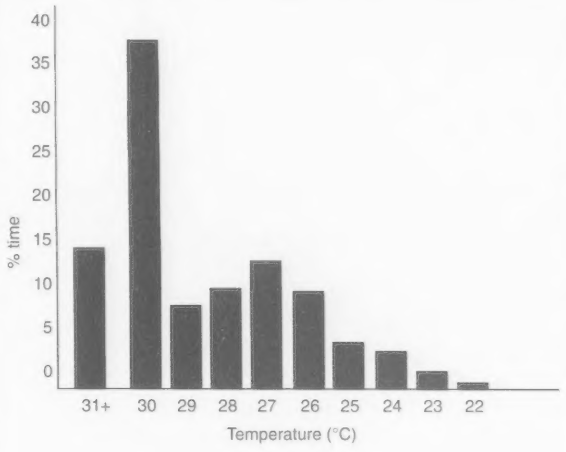

Figure 4

Distribution of time at temperature for eight of nine blue marlin equipped with pop-up satellite tags near Bermuda, 25 July–11 August 1999. Histogram represents combined data for the five-day period of data transmission for each individual.

lin than that recommended by the manufacturer, at least in the short term. Thus a pop-up tag of this size might be tested on even smaller specimens or other target species to expand the study of behavior in a wider size range of species than was originally thought possible.

Acknowledgments

The authors would like to thank Captains Alan DeSilva, Andrew Card, Gilbert Amaral and Bobby Rego for providing assistance in deploying the pop-up tags. We also express our appreciation to the anglers and to the organizing committee of the Bermuda Billfish Tournament for their support. Paul Howey and Molly Lutcavage provided expert technical advice. Phil Goodyear made helpful comments on the manuscript. Support for this project was obtained from the Bermuda Department of Agriculture and Fisheries, the ICCAT Enhanced Research Program for Billfish, and Hewit Family Foundation.

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Reproduction of the blacknose shark (*Carcharhinus acronotus*) in coastal waters off northeastern Brazil

Fabio H. V. Hazin
Paulo G. Oliveira
Matt K. Broadhurst

Departamento de Pesca, Laboratório de Oceanografia Pesqueira
Universidade Federal Rural de Pernambuco
Av. Dom Manuel de Medeiros, s/n
Dois Irmãos, Recife-PE, Brasil, CEP: 52.171-900
E-mail address (for F. Hazin): fhvhazin@elogica.com.br

The blacknose shark, *Carcharhinus acronotus*, is a relatively small carcharinid, typically inhabiting continental shelf areas in the western Atlantic Ocean, from North Carolina throughout the Gulf of Mexico (Bigelow and Schroeder, 1948) and along the South American coast to Rio de Janeiro (Compagno, 1984). The abundance of this shark in nearshore areas throughout its distribution makes it accessible to commercial fishing, mainly from inshore hook-and-line and gill-net fisheries (Trent et al., 1997; Mattos and Hazin[1]).

Aspects of the biology of *C. acronotus* have been reported by Springer (1938); Bigelow and Schroeder (1948); Clark and von Schmidt (1965); Dodrill (1977); Branstetter (1981); Schwartz (1984); Castro (1993); and Carlson et al. (1999). Schwartz (1984) provided the most comprehensive synopsis, including information on their reproduction and life cycle off North Carolina. Many of the other studies were based on relatively few specimens collected off the southeastern United States and corroborate much of Schwartz's (1984) work, including patterns in spatial and temporal abundances, size at maturity, fecundity, and time of parturition. However, some inconsistencies exist with respect to the duration of the ovarian, gestation, and breeding cycles: i.e. Dodrill (1977) proposed a biennial breeding cycle with gestation taking between 10 and 11 months, Schwartz (1984) suggested a gestation of approximately 9 months, and Branstetter (1981) observed two gravid females with large ovarian eggs (having concurrent ovarian and gestation cycles, copulation having occurred shortly after parturition).

Because *C. acronotus* are represented in catches from various inshore fisheries and carcharhinids typically are characterized by low rates of population increase, adequate information about their reproductive cycle is required to facilitate management of stocks. Given the uncertainty of knowledge about reproduction in *C. acronotus* and the lack of information for the southern part of their range, our aims in the present study were to provide a preliminary overview of the reproductive biology and life cycle of the blacknose shark in coastal waters off northeastern Brazil, using available fishery-dependent data.

Material and methods

Fishing gear used and data collected

Carcharhinus acronotus (79 females and 45 males) were collected from the catches of commercial gillnetters and vessels using bottom longlines off the coast of northeastern Brazil (approx. 7°30′ to 9°30′S—near Recife) between August 1994 and January 1999. The configuration of fishing gears used remained similar over this period. Gill nets were monofilament, 900 m in length, and had a stretched mesh size of 17 cm and a depth of 70 meshes. Nets were set perpendicular to the beach at depths between 5 and 10 m. Bottom longlines consisted of a multifilament mainline (6 mm in diameter) with up to 100 secondary lines, each approx. 5 m in length and constructed from 3-mm diameter monofilament attached to a wire snood (1 m in length). Types of hooks varied among brands, but relative sizes (i.e. 9/0) remained similar. The main baits were sardine (*Sardinella brasiliensis*) and mackerel (*Scomber* spp.), although some other species, including sting ray (*Aetobarus narinari*) and skipjack tuna (*Katsuwonus pelamis*) were occasionally used. Longlines were set on the continental shelf at depths between 10 and 60 m, but most sets were shallower than 40 m. All fishing gears were set at dusk and hauled the following morning at dawn.

All specimens were measured (total length [TL] in the natural position) and dissected. Reproductive organs were removed and stored in a solution of 10% formalin in seawater prior to being transported to the laboratory. Data collected from females included weight and width of the oviducal gland and the functional right ovary, maximum ovarian follicle diameter (MOFD), width of the largest uterus, and, if present, the TL, sex, and number of embryos. Using the methods described by Pratt (1993), we examined the oviducal glands of 10 mature females for the presence of spermatozoa. Length and calcification stage of claspers, width of epididymides, and the presence of seminal fluid in the ampullae of the ductus deferens were recorded from males. Reproductive organs were measured to the nearest 0.1 mm with vernier calipers.

Inferences on stages of reproduction were made according to definitions provided in previous studies on carcharinids (e.g. Pratt, 1979; Hazin et al., 2000). Females were categorized into six stages, mainly based on develop-

[1] Mattos, S. M. G. and F. H. V. Hazin. 1997. Análise de viabilidade econômica da pesca de tubarões no litoral do estado de Pernambuco. Boletim Técnico-científico do Cepene, 5: 89–114. IBAMA (Instituto Brasiliero de Meio Ambiente e dos Recursos Naturais Renováveis), Rua Samuel Hardman, s/n Tamandaré – PE, Brazil.

Manuscript accepted 5 July 2001]
Fish. Bull. 100:143–148 (2002).

ment of the oviducal gland, ovary, and uterus. Specimens were considered juvenile if they had undeveloped sexual organs, filiform uteri, and no vitellogenic activity in their ovaries. Pre-ovulatory females had relatively larger ovaries with orange vitellogenic follicles, but no uterine eggs. Ovulating females had uterine eggs and ripe ova still in the ovary, whereas in gravid specimens ovulation was complete. Postpartum females showed similar-size ovaries, oviducal glands, and ovarian follicles as those of gravid specimens, but had flaccid uteri that were still slightly enlarged (compared with other nongravid females) indicating recent parturition. Individuals that had similar-size uteri as those of pre-ovulatory and ovulating individuals, but smaller ovarian follicles with little or no vitellogenic activity were termed "resting" females. Male maturation was evaluated according to development of the testes and claspers. Individuals with relatively short, flexible claspers, and filiform ampullae of the ductus deferens were considered juveniles. Adults were characterized by elongate and calcified claspers and relatively large epididymides (compared with juveniles).

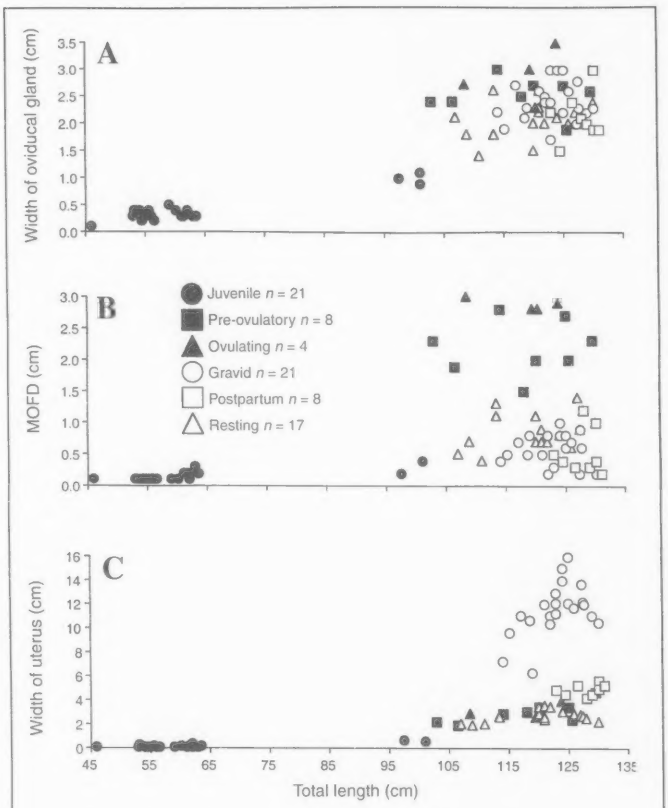

Figure 1

Relationship between total length and (**A**) width of oviducal gland, (**B**) MOFD (maximum ovarian follicle diameter), and (**C**) width of uterus.

Statistical analyses

Size-frequency distributions of males and females were compared by using a two-sample Kolmogorov-Smirnov test (P=0.05). Chi-squared goodness-of-fit tests were used to examine the hypothesis of an equal sex ratio between numbers of juvenile and adult *C. acronotus* sampled and among embryos in gravid females. To help define time of parturition, analysis of variance (ANOVA) was used to investigate the hypothesis of an increase in TL of embryos from near-term females captured in November and December. To provide a balanced analysis, three gravid females captured on 10 December 1998 were analyzed with three individuals captured almost one month earlier on 11 November 1998. Data were assessed for normality by using the Shapiro and Wilk procedure (Zar, 1996), tested for heteroscedasticity with Cochran's test, and then analyzed in the appropriate one-nested factor ANOVA (Underwood, 1981). Gravid females were considered a random-effects factor nested in months and the four embryos for each gravid female were the replicates.

Results

The Kolmogorov-Smirnov test detected significant differences in size-frequency compositions between males and females; proportionally more larger-size females (121–131 cm TL) were captured. Both sexes showed two distinct cohorts. The first consisted of juveniles (46–65 cm) captured by gill nets at depths between 5 and 10 m, and the second included larger specimens (i.e. 85–131 cm), and mostly adults, captured on bottom longlines in deeper water (10 to 60 m). The ratio of juvenile males to females was not significantly different from 1:1 (χ^2=0.027, P>0.01), whereas significantly fewer adult males than females were sampled (ratio of 1:2.34) (χ^2=14.08, P<0.01).

Female maturation and reproduction

Juveniles ranged in size from 46 to 101 cm TL and had narrow oviducal glands, light ovaries with undeveloped white follicles, and thin uteri (Fig. 1, A–C, Table 1). Pre-ovulatory specimens ranged in size from 103 to 129.5 cm TL, had well-developed oviducal glands (width of between 1.9 and 3 cm), and mature ovaries with thick orange follicles (1.5 to 2.8 cm in diameter) (Fig. 1, A and B, Table 1). The shortest pre-ovulatory specimens (e.g. 103 and 106 cm TL), had oviducal glands that were substantially wider (i.e. >2×) than those in the longest juveniles (101 cm TL) (Fig. 1A, Table 1); therefore sexual maturity probably was approached within this size range. This should be con-

Table 1

Characteristics of female *C. acronotus* in each maturation stage and the total length (TL) range and number of specimens. All widths and lengths are in cm, weights in g. MOFD = maximum ovarian follicle diameter.

Characteristic	Juvenile	Pre-ovulatory	Ovulating	Gravid	Postpartum	Resting
Width of oviducal gland	<1.1	1.9–3.0	2.3–3.5	1.7–3.0	1.5–3.0	1.4–2.6
Weight of oviducal gland	2.2–3.0	5.7–8.7	8.6–10.0	2.3–5.0	3.0–5.0	3.0–7.7
Width of uterus	<0.7	1.9–4.7	2.6–3.9	6.3–16	4.2–5.6	1.9–3.5
MOFD	0.1–0.4	1.5–2.8	2.8–3.0	0.2–1.0	0.2–1.2	0.4–1.4
Width of ovary	0.4–1.7	2.3–6.0	4.9–5.7	1.5–3.8	2.2–3.5	1.7–4.0
Weight of ovary	2.7–4.6	12.2–18.2	20.0–24.6	4.5–16.5	12.0–23.0	4.97–16.5
TL of specimens	46.0–101.0	103.0–129.5	108.5–123.8	114.0–130.0	123.0–131.0	107.0–130.0
Number of specimens	21	8	4	21	8	17

sidered a preliminary estimate of size at sexual maturity because few individuals were caught between 95 and 105 cm TL and none between 75 and 95 cm TL. Compared with pre-ovulatory females, those in the process of ovulation had slightly wider oviducal glands and heavier ovaries with thicker follicles (2.8–3 cm in diameter) (Fig. 1, A and B, Table 1). Ovulation appeared to occur only when MOFD was at least 2.8 cm (Fig 1B). The majority of gravid, postpartum, and resting females ranged in size from 111 to 131 cm TL and had similar-size oviducal glands (Fig. 1A, Table 1). Gravid females had undeveloped ovaries with no vitellogenic activity (MOFD was less than 1 cm). Uteri in postpartum females were flaccid and slightly distended (4.2–5.6 cm in width), whereas uteri of resting females were comparable to pre-ovulatory and ovulating individuals (Fig. 1C, Table 1). No mating scars were observed on any of the females. There was no evidence of spermatozoa stored in the oviducal glands of 10 females examined.

The temporal abundance of females according to stages of reproduction showed that juveniles were present in catches between January and November, but mainly from February to June (Fig. 2A). Pre-ovulatory and ovulating individuals were sampled between February and April and April and May, respectively (Fig. 2A). Except for one gravid female caught during August, all gravid, postpartum, and resting females were caught between November and January (Fig. 2A). MOFD of mature females was lowest in August and between November and January, after which it steadily increased to May (Fig. 2B).

Examination of the uterine contents of the 22 gravid females (Table 2) revealed that individual litter size was always four with both sexes present in varying proportions, although the total pooled ratio of males to females (1:1.25) was not significantly different from 1:1 (χ^2=1.13, P>0.05). All embryos from individual gravid females were at similar stages of development and showed small variation in TL. ANOVA detected significant differences in mean TLs of embryos among near-term females (F=20.51, P<0.01) and for the main effect of months (F=10.45, P<0.05). ANOVA showed that the mean (±SE) TL of embryos in three near-term females caught on 10 December 1998 (45.96 ±0.38 cm) was significantly longer than in three near-term females caught on 11 November 1998 (42.31 ±0.07 cm), suggesting that embryos continued to develop between these periods.

Table 2

Date of capture and total length (TL) of gravid *C. acronotus* and the mean TL (±E) and sex ratio of embryos.

		Embryos	
Date of capture	TL of gravid specimen	Mean TL (±SE)	Males: females
17 Aug 94	118.6	29.15 (1.23)	1:3
11 Nov 98	121	42.50 (0.14)	1:3
11 Nov 98	122	45.32 (0.60)	2:2
11 Nov 98	123	40.75 (0.25)	3:1
11 Nov 98	125	43.25 (0.43)	3:1
11 Nov 98	129	45.12 (0.43)	3:1
13 Nov 98	130	38.50 (2.06)	2:2
17 Nov 98	114	34.27 (0.19)	3:1
17 Nov 98	127.7	42.50 (0.15)	3:1
21 Nov 98	115.2	41.37 (0.37)	3:1
22 Nov 98	127.2	45.47 (0.62)	2:2
25 Nov 98	126	43.87 (2.01)	2:2
25 Nov 98	127.5	46.07 (0.22)	1:3
6 Dec 98	117	44.75 (0.14)	2:2
6 Dec 98	123	43.37 (0.85)	2:2
6 Dec 98	123	48.50 (0.28)	2:2
7 Dec 98	125	46.87 (0.12)	2:2
10 Dec 98	124	45.62 (0.37)	2:2
10 Dec 98	124	47.50 (0.28)	3:1
10 Dec 98	122	44.75 (0.25)	2:2
12 Dec 98	123	42.50 (0.35)	3:1
5 Jan 95	114.5	45.37 (0.24)	2:2

Male maturation and reproduction

Of the 45 males examined, 23 were juvenile with thin epididymides (Fig. 3A) and filiform ampullae of the ductus deferens without seminal fluid. Juveniles ranging from 49

to 63 cm TL had relatively short flexible claspers (Fig. 3B) and testes that were not fully differentiated from the epigonal organ. No males between 64 and 87 cm TL were caught. Three juveniles (88, 93, and 94 cm TL) had claspers that were enlarged and beginning to calcify (Fig. 3B) and two larger specimens also had thick epididymides (Fig. 3A). Males appear to approach sexual maturity before 104 cm TL because all specimens longer than this had completely developed sexual organs, including elongate and calcified claspers, thick epididymides, and circumvoluted ampullae of the ductus deferens (Fig. 3).

Discussion

Prevalence of adult females in catches was similar to that from observations made by Schwartz (1984) for stocks off the southeastern United States and can be attributed to a reproductive migration involving relatively large numbers of gravid individuals (114 to 130 cm TL) into the sampled area. Because there was no evidence of disequilibrium between sexes (i.e. there were equal numbers of male and female embryos and juveniles), large numbers of adult males were probably segregated. It is unlikely males were in the sampled area and not caught because females, although proportionally larger, were captured across the same size range (Fig. 1), implying that the selectivity of the gear encompassed the range of sizes of males.

Evaluation of the maturation stages of males and females showed delineation between juveniles and adults. All females longer than 103 cm TL had enlarged oviducal glands and developed ovaries (Fig. 1, A and B, Table 1), and males longer than 104 cm TL had elongate and calcified claspers and thick epididymides (Fig. 3), indicating that sexual maturity was probably approached at these lengths. Although these estimates were derived from few individuals, they are comparable to those proposed by most researchers for specimens collected off the southeastern United States (e.g. Springer, 1938; Clark and von Schmidt, 1965; Compagno, 1984), with the exceptions of Branstetter (1981) who suggested 110 cm TL for both sexes and Schwartz (1984) who suggested 110 cm TL for males.

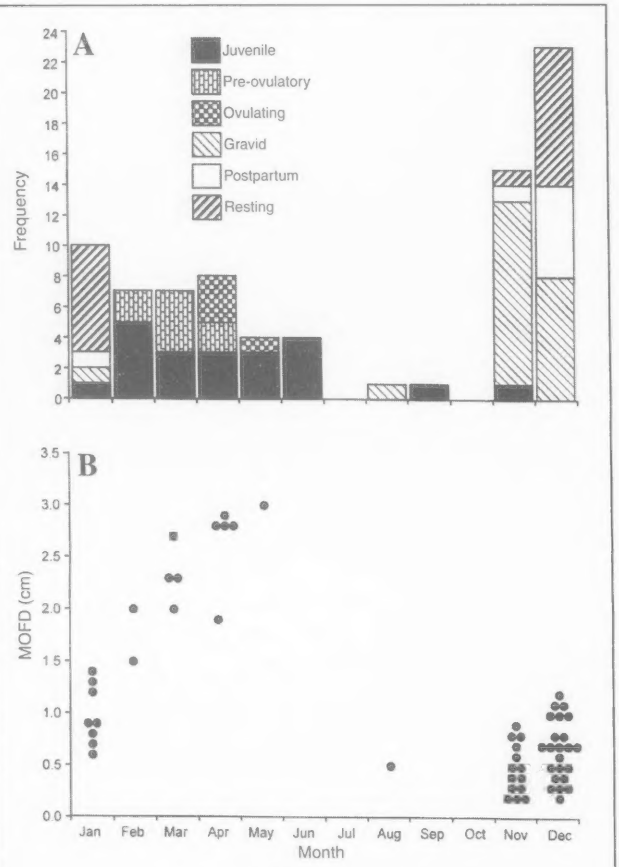

Figure 2

Monthly distribution of (**A**) females in catches according to their stage of reproduction and (**B**) MOFDs (maximum ovarian follicle diameters) for mature females.

Size at birth, number of embryos, sex ratio of embryos, and the time of parturition of *C. acronotus* in our study are consistent with corresponding data from earlier works (Springer, 1938; Clark and von Schmidt, 1964; Dodrill (1977); Branstetter, 1981; Compagno, 1984; Schwartz, 1984). Size at birth has been suggested to be between 45 and 50 cm TL (e.g. Branstetter, 1981; Castro, 1993) and litter sizes commonly range from 3 to 6 (Springer, 1938; Dodrill, 1977; Compagno, 1984). We observed gravid females caught in November and December (late spring to early summer) with embryos longer than 45 cm TL (Table 2). Given the significant increase in size of embryos between these months (indicating that embryos were still developing) and the capture of several neonates (46–51 cm TL) in February and March (late summer to early autumn), we conclude that parturition off northeastern Brazil probably occurs from December to January (mid to late summer). A similar seasonal timing has been proposed for stocks off the southeastern United States (e.g. during June—Schwartz, 1984) and is generally typical for the majority of carcharhinids (e.g. Castro, 1993).

In contrast to the inference made by Branstetter (1981) but in agreement with observations of Schwartz (1984), we showed that vitellogenisis and gestation occur consecutively in *C. acronotus*. Ovaries of adult females off northeastern Brazil begin to mature (pre-ovulatory stage) in February (late summer) with ovulation occurring two to three months later (Fig. 2, A and B). This sequence of events is illustrated by a rapid increase in MOFD from February (1.5–2 cm in diameter) to May (3 cm in diameter) (Fig. 2B). Given the proposed summer parturition (December to Janu-

ary), mating and fertilization during April and May (autumn) would result in a gestation period of approximately 8 months—slightly shorter than that suggested by Schwartz (1984) and Dodrill (1977) (9 and 10 to 11 months, respectively) for stocks off the southeastern United States. Further, the periods required for vitellogenisis and gestation indicate that reproduction of *C. acronotus* off northeastern Brazil could be completed within 10 to 11 months.

With the simultaneous capture of nongravid and gravid females off Florida, Dodrill (1977) proposed a biennial reproductive cycle for *C. acronotus*. Although we also collected gravid and nongravid (i.e. postpartum and resting) females together (i.e. mostly during December and January), the latter individuals could have given birth 3 or 4 weeks earlier. If these females subsequently ovulated 2 months later (in April), then reproduction could conceivably be annual. A fast vitellogenic period, combined with clear reproductive progress, is also supportive of a 1-year cycle. An alternative hypothesis that supports biennial reproduction is that the resting females represented some proportion of segregated nongravid females that moved with the relatively large numbers of gravid females into the parturition area. Given the lack of adult females in catches between June and November (winter to late spring), it is likely, however, that they frequent other areas after copulation. Without additional fishery-independent data, it is impossible to determine these locations and whether some proportion of the female population consists of nongravid or resting individuals throughout the year.

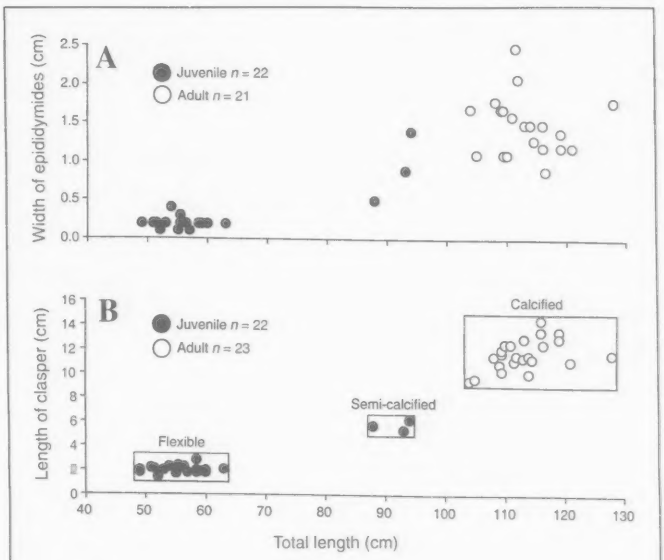

Figure 3

Relationships between total length and (**A**) width of epididymides and (**B**) length of clasper.

Our evidence suggests a shorter reproductive cycle for *C. acronotus* than that previously noted in the literature. Given the 6-month difference between times of ovulation and parturition for females off northeastern Brazil and those off the southeastern United States, our results also indicate the existence of at least two separate stocks. Noting temporal differences in the sizes of embryos from females, Schwartz (1984) proposed two partially separated populations off the southeastern United States: one off North Carolina and the other comprising individuals from Florida and the Gulf of Mexico. Additional research is needed to determine if the population in the southwestern Atlantic is separate from those in the north because the existence of a unit stock off northeastern Brazil would require separate management measures according to the status of that stock.

Acknowledgments

This study was funded by the Comissão Interministerial para os Recursos do Mar (CIRM) through the Programa Nacional de Avaliação dos Recursos Vivos da Zona Econômica Exclusiva (REVIZEE), the Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco (FACEPE), and the Conselho Nacional de Ensino e Pesquisa (CNPq). We thank T. Souza, H. Requiaõ, P. Pinheiro, and L. Wojciuk for technical assistance and R. Lessa for critically reading the manuscript.

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A new growth model for red drum (*Sciaenops ocellatus*) that accommodates seasonal and ontogenic changes in growth rates

Clay E. Porch
Southeast Fisheries Science Center
75 Virginia Beach Drive
Miami, Florida 33149-1099
E-mail address: Clay.Porch@noaa.gov

Charles A. Wilson
David L. Nieland
Coastal Fisheries Institute
School of the Coast and Environment
Louisiana State University
Baton Rouge, Louisiana 70803

The red drum (*Sciaenops ocellatus*) is a popular gamefish found throughout the coastal waters of the Gulf of Mexico and along the eastern seaboard as far north as Massachusetts. Juvenile red drum grow extremely rapidly, especially during the warmer months, but adults grow very little. In fact, the change in growth with age is so abrupt that the standard von Bertalanffy curve has proven inadequate—the predicted lengths of younger fish are generally too large and the predicted lengths of older fish too small (see Beckman et al., 1988; Murphy and Taylor, 1990).

Two generalizations of the von Bertalanffy curve have been found to fit red drum length-at-age data better than the original three-parameter form. The first, dubbed the "double" von Bertalanffy growth curve (Vaughan and Helser, 1990; Condrey et al.[1]), allows the rate at which an animal approaches the asymptotic length to change after some pivotal age, t_p:

$$l_t = \begin{cases} l_\infty\left(1-e^{-k_1(t-t_1)}\right) & \text{if } t < t_p \\ l_\infty\left(1-e^{-k_2(t-t_2)}\right) & \text{if } t \geq t_p \end{cases} \quad (1)$$

$$t_p = (k_2 t_2 - k_1 t_1)/(k_2 - k_1),$$

where t = age;
l_∞ = asymptotic length;
k_1, k_2 = instantaneous growth rate coefficients; and
t_1, t_2 = age intercept parameters.

The second, dubbed the "linear" von Bertalanffy curve (Hoese et al., 1991; Vaughan, 1996), expresses the asymptotic length as a linear function of age:

$$l_t = (b_0 + b_1 t)(1-e^{-k(t-t_0)}). \quad (2)$$

Of course other generalizations of the von Bertalanffy curve may also be appropriate, such as the Richards (1959) equation

$$l_t = l_\infty(1-\delta e^{-k(t-t_0)})^{\frac{1}{\delta}} \quad \text{where } \delta \neq 0. \quad (3)$$

The double von Bertalanffy curve accommodates the possibility that older, larger fish might grow more slowly in proportion to their length than younger, smaller fish. (The linear von Bertalanffy curve has no biological interpretation.) In reality, one might expect the growth rate in proportion to length to decrease gradually with the age of the fish rather than at some abrupt pivotal point. Moreover, the growth pattern of juvenile red drum seems to have a strong seasonal component (Goodyear[2]). In this paper a new growth equation is developed that explicitly models these two features. The new equation provided a better fit to northern Gulf of Mexico red drum age-length data than any of the above alternatives.

Materials and methods

The model

The growth rate at any given age t is assumed to be in some proportion k to the difference between the expected size at that age (l_t) and the expected maximum (l_∞):

$$\frac{dl_t}{dt} = k(l_\infty - l_t). \quad (4)$$

Further, k is assumed to decline with age and vary with the seasons such that

$$k = k_0 + k_1 e^{-\lambda_1 t} + k_2 e^{-\lambda_2 t}\sin(2\pi(t-t_c)), \quad (5)$$

where λ_1 and λ_2 are damping coefficients and t_c is a shifting parameter for the sine wave valued between 0 and 1. Substituting Equations 5 and 4 and integrating with $l = 0$ when $t = t_0$ gives

[1] Condrey, R., D. W. Beckman and C. A. Wilson. 1988. Management implications of a new growth model for red drum. Appendix D. *In* Louisiana red drum research, J. A. Shepard (ed.), 26 p. U.S. Dept. Commerce Cooperative Agreement NA87-WC-H-06122. Marine Fisheries Initiative (MARFIN) Program. Louisiana Department of Wildlife and Fisheries, Seafood Division, Finfish Section, Baton Rouge, Louisiana 70803-7503.

[2] Goodyear, C. P. 1996. Status of the red drum stocks of the Gulf of Mexico: report for 1996. Rep. MIA 95/96-47, 21 p. Miami Laboratory, Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 75 Virginia Beach Dr., Miami, Fl. 33149.

Manuscript accepted 17 May 2001.
Fish. Bull. 100:149–152 (2002).

$$l_t = l_\infty(1-e^{\beta_1+\beta_2-k_0(t-t_0)})$$

$$\beta_1 = \frac{k_1}{\lambda_1}(e^{-\lambda_1 t} - e^{-\lambda_1 t_0})$$

$$\beta_2 = \frac{k_2}{4\pi^2+(\lambda_2)^2}\left[\begin{matrix} e^{-\lambda_2 t}\left(\begin{matrix}2\pi\cos\{2\pi(t_c-t)\}-\\ \lambda_2\sin\{2\pi(t_c-t)\}\end{matrix}\right)- \\ e^{-\lambda_2 t_0}\left(\begin{matrix}2\pi\cos\{2\pi(t_c-t_0)\}-\\ \lambda_2\sin\{2\pi(t_c-t_0)\}\end{matrix}\right)\end{matrix}\right]. \quad (6)$$

Assuming the animal will not shrink with age, i.e., $dl/dt \geq 0$, implies the constraint

$$k_0 + k_1 e^{-\lambda_1 t} + k_2 e^{-\lambda_2 t}\sin(2\pi(t-t_c)) \geq 0. \quad (7)$$

Equation 6 may appear formidable, but typically requires only a minute or two more to enter into standard statistical fitting packages. It reduces to a form similar to the Gompertz equation when $k_2 = 0$ and to the von Bertalanffy equation when $k_1 = k_2 = 0$.

Fitting the model to data

Equations 1, 2, 3, and 6 were fitted to observations of length-at-age from red drum collected in the northern Gulf of Mexico between September 1985 and October 1998 (see Beckman et al., 1988, or Wilson et al.[3] for further details regarding the data collection and aging procedures). The fitting was accomplished by ordinary least squares by using a Nelder-Mead simplex search[4] and, as a check, proc NLIN of SAS (1990). The least-squares solution is equivalent to the maximum likelihood solution when the distribution of length at age is normal with constant variance, which seems to be approximately true of this particular data set (Porch, unpubl. data).

Akaike's (1973) information criterion (AIC) was used to rank the growth models in terms of their ability to provide statistically parsimonious explanations of the data. The formula for the AIC may be written

$$AIC = -2\log(L) + 2p,$$

where L is the likelihood function and p is the number of parameters (see Buckland et al., 1997). In this case, $-2\log(L)$ is equal to the residual sums of squares.

[3] Wilson, C. A., D. L. Nieland and A. L. Stanley. 1993. Variation of year-class strength and annual reproductive output of red drum *Sciaenops ocellatus* and black drum *Pogonias cromis* from the northern Gulf of Mexico. Final Report 1991–1992, 31 p. U.S. Dept. Commerce Cooperative Agreement NA90AA-H-MF724. Marine Fisheries Initiative (MARFIN) Program. Coastal Fisheries Institute. Louisiana State University, Baton Rouge, La 70803-7503.

[4] Shaw, D. E., R. W. M. Wedderburn, and A. Miller. 1991. A Program for function minimization using the simplex method. CSIRO, Division of Mathematics and Statistics, P.O. Box 218, Lindfield, N.S.W. 2070, Australia.

Table 1

Akaike's information criteria (AIC) quantifying the fit of the various growth models to the red drum length-at-age data. Smaller AIC values indicate statistically better fits.

Model	Number of parameters	Negative log-likelihood	AIC (–25,000)
von Bertalanffy	3	16045.9	7098
Richards	4	14169.8	3348
linear von Bertalanffy	4	12883.8	776
double von Bertalanffy	5	12876.6	763
damped (Eq. 6, k_2=0)	5	12651.3	313
seasonal + damped (Eq. 6)	8	12584.9	186

The parameter estimates for the Richards equation tended to be unstable unless good initial estimates were provided. This was accomplished by conducting the estimation in two stages. In the first stage the exponent δ was fixed to 1 and the other parameters were estimated, reducing the Richards equation to the von Bertalanffy form. In the second stage the initial guesses were set equal to the final estimates from the first stage and then all four parameters were estimated simultaneously.

Results and discussion

All five alternative growth models fitted the data significantly better than the von Bertalanffy equation according to the AIC statistic (Table 1). The Richards equation, however, did not fit the data nearly as well as the other alternative formulations and suffered from well-known instability problems (Ratkowsky, 1983), therefore it can probably be dropped from any future consideration with respect to red drum. The double von Bertalanffy curve fitted the data better than the linear von Bertalanffy curve, but the comparison is rendered moot by the performance of the new model. The five-parameter version without seasonal oscillations (Eq. 6 with k_2=0) fitted the data significantly better than either. The eight-parameter version with seasonal oscillations fitted the data significantly better still (see Fig. 1).

The estimated seasonal component to the growth rate was fairly substantial initially, having an amplitude at age 0 of 0.301 (k_2) and a peak in June, but declined rapidly with age (Fig. 2). It is possible that an even stronger seasonal signal would have been estimated if age-0 fish, which exhibit the strongest seasonal pattern (Goodyear[4]), had been adequately represented in the sample.

Some of the parameter estimates were highly correlated, as is the case in most growth studies. In particular, the correlations between the estimates for the growth rate and asymptotic length coefficients were typically above 0.8. However, the asymptotic variance-covariance matrix

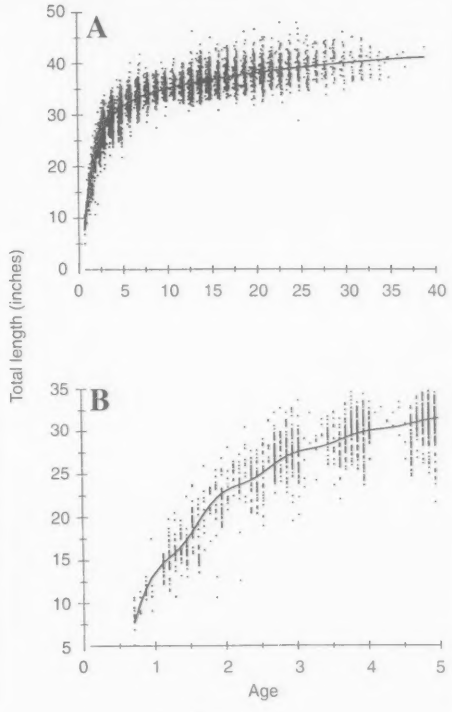

Figure 1

Fit of the proposed seasonal growth model to red drum length at age data: (**A**) the fit for all ages; (**B**) the fit for the younger ages.

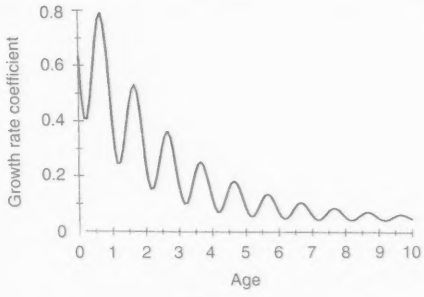

Figure 2

Growth rate coefficient from seasonal model as a function of age.

suggests that the parameters for all of the models were estimated fairly precisely (Table 2).

The new model, either with or without the seasonal component, has both practical and theoretical advantages over the four other models examined in this study. By virtue of its greater flexibility, it was able to fit the red drum data significantly better than the linear and double von Bertalanffy curves (its nearest competitors). Moreover, the Richards and linear von Bertalanffy curves are theoretically disadvantaged because their parameters have no physical interpretation. The double von Bertalanffy curve, although it has a physical interpretation, suffers because it allows only a single discontinuous change in the growth rate at one age rather than a continuous change through time. For these reasons, the new model should be more widely applicable than the others, particularly for species that change habitat preferences with age or are subject to strong seasonal environmental fluctuations.

Table 2

Parameter estimates and corresponding coefficients of variation (CV) derived from the asymptotic covariance matrix.

Model	Parameter	Estimate	CV (%)
von Bertalanffy	l_∞	37.7	1
	k	0.323	1
	t_0	–0.646	3
linear von Bertalanffy	b_0	32.5	1
	b_1	0.284	1
	k	0.590	9
	t_0	0.126	1
double von Bertalanffy	l_∞	40.0	1
	k_1	0.412	1
	t_1	0.0530	23
	k_2	0.114	2
	t_2	–8.41	3
damped (Eq. 6, k_2=0)	l_∞	44.1	1
	k_0	0.0416	7
	t_0	0.362	3
	k_1	0.667	2
	λ_1	0.464	1
seasonal and damped	l_∞	43.4	1
	k_0	0.0475	5
	t_0	0.443	3
	k_1	0.695	2
	λ_1	0.476	1
	k_2	0.301	16
	λ_2	0.344	22
	t_c	0.439	3

Acknowledgments

We thank C. Legault, G. Scott, S. Turner, D. Vaughan, and an anonymous reviewer for their helpful comments.

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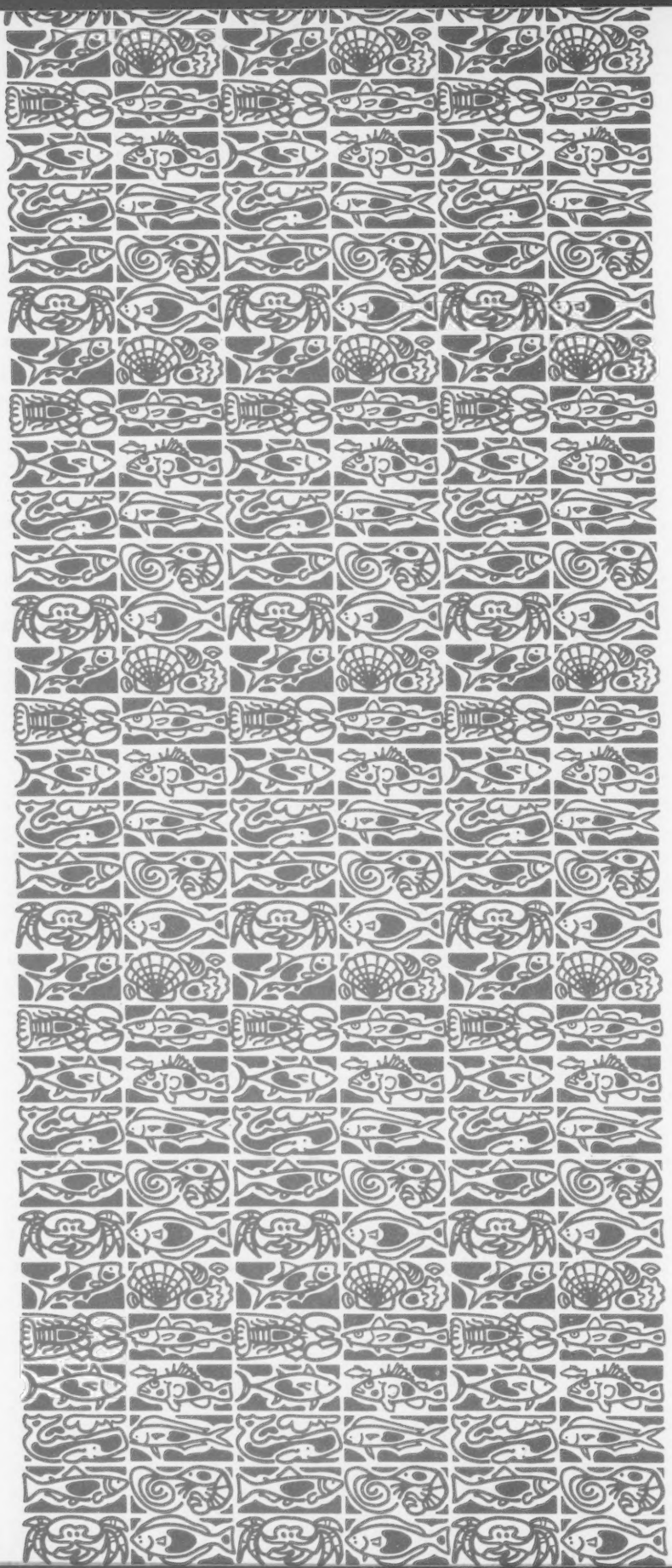
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